Studies of social behaviour involving contact in the young of four rodent species

Thesis

STUDIES OF SOCIAL BEHAVIOUR INVOLVING CONTACT IN THE YOUNG OF FOUR RODENT SPECIES

by

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ABSTRACT

Social behaviour involving contact among littermates and between parents and young has been studied and compared in two species of microtine rodents and two species of caviomorph rodents. Parent-young contact and juvenile interactions involving body nosing, allogrooming and play were recorded.

One species each of the microtine and caviomorph rodents was believed from earlier studies of adult social behaviour to be more socially tolerant and communal than the other; this study explored the hypothesis that the two more tolerant species, Microtus ochrogaster and Octodon degus, would differ from their counterparts Microtus pennsylvanicus and Octodontomys gliroides respectively with regard to the juvenile and parent-young behaviours observed. It was found that in M. ochrogaster both parents spent more time in contact with their young than in M. pennsylvanicus. Further, young M. ochrogaster displayed more body nosing, allogrooming and sitting in contact, and more reciprocity in their interactions than did M. pennsylvanicus. Octodon parents and young engaged in more contact behaviours such as huddling, allogrooming and forepaw-clasping than did Octodontomys, whereas Octodontomys displayed more frequent and vigorous locomotor and rotational movements than did Octodon. In Octodon, the father tended to dominate father-young interactions,

and young interacted less with each other and their mother in his presence than in his absence; such paternal dominance was not evident in Octodontomys.

Although the social behaviour repertoire was similar in the Microtus and the caviomorph young, some differences in the use of the repertoire were predicted owing to differences between the two groups in phylogeny, and the relatively greater longevity, lower rate of reproduction, and greater ability for complex learning in these caviomorphs. Two major relevant differences were found when Octodon and M. ochrogaster were compared: there was more physical manoeuvering (such as mutual-upright interaction and forepaw-clasping) in the play of Octodon young, and spontaneous interaction levels among siblings were greater in Octodon. These and other differences may relate to the development of more complex social relationships in these caviomorphs than in the Microtus.

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This thesis presents the results of an investigation into the ways in which the young of four rodent species use nosing of the body and bodily contact during non-aggressive interactions with their parents and conspecific young. Although the study was carried out in captivity, environmental conditions were created which were believed to be appropriate for promoting the natural behaviour of the young of each species.

Two different kinds of rodent were selected for the study of juvenile and parent-young behaviour. Two North American species of vole (Cricetidae: Microtus ochrogaster and Microtus pennsylvanicus) were chosen. These are small rodents (adult body weight ca. 30g), are relatively short-lived (life span in captivity of about a year), have a short gestation (three weeks), and may exhibit continuous breeding over several months. Two species of South American caviomorph rodent (Octodontidae: Octodon degus and Octodontomys gliroides) were also selected. These are medium-sized rodents (adult body weight ca. 250g and 200g in Octodon and Octodontomys respectively), are relatively long-lived (life-span in captivity of about five years), have a long gestation (12 weeks in Octodon, 15 weeks in Octodontomys), and give birth only once or twice a year. Whereas the genus Microtus includes 44 species having a combined range covering much of North America and the northern Eurasian continent, the genus Octodon has only three species, all confined in occurrence to

Chile, and Octodontomys gliroides is the only species in the genus, limited in its range to mountainous areas of Chile, Bolivia and Argentina (Walker, 1975).

Although microtine and octodontid species are different phylogenetically, physically and ecologically, they have been found to share in common certain juvenile social behaviour patterns including repetitive sniffing and grooming of the snout, neck and rump regions, dyadic interactions in the mutual-upright position, and rapid jumping, zig-zag running, and head-shaking (locomotor-rotational 'play' movements). In an earlier study of a British vole species (Microtus agrestis; Wilson, 1973), I found that young or sexually immature voles frequently engaged each other in nosing of the three above-mentioned body regions. This behaviour occurred repeatedly during dyadic encounters between strangers, leading ultimately to extensive bodily contact and nest-sharing. Similar repetitive body nosing also occurred on the part of cohabiting littermates during activity periods; in this context the young often nosed one another while moving around the enclosure. Locomotor-rotational 'play' movements often occurred in this context. An animal would give a play movement usually just before or after nosing a companion, but sometimes also when moving past a littermate. During this study I was able to extract a substance from the skin surface of the neck of young voles; when such an extract was offered to a litter (on a cotton ball and on the neck of a litter member), the litter repeatedly nosed it and gave more play movements than normal. Subsequent observations of caviomorph rodent young in litter groups (Wilson and Kleiman, 1974) suggested that in

these animals also, body nosing among siblings as they moved around during activity periods often led to locomotor-rotational 'play' movements and mutual-upright 'play' interactions. In Octodon and Octodontomys most (more than 80%) rotational movements (head-shaking and body twisting) and more than half of play jumps occurred immediately upon nosing the body of another animal (sibling or parent). In both species, nosing of the neck area was the behaviour most frequently preceding these play movements.

These similarities between the Microtus and the caviomorphs with respect to juvenile social interactions and play prompted the present more detailed study of juvenile social behaviour and its ontogeny in both types of rodent. Whereas these earlier studies focussed mainly on play behaviour among littermates, and especially on nosing of the body as a stimulus for locomotor-rotational movements, the present study encompasses all forms of contact observed to occur between the young rodent and its parents and peers. Body nosing exchanges, interactions involving physical manoeuvering (such as the mutual-upright) and locomotor-rotational movements are frequent while the animals are actively moving around, social grooming (allogrooming) tends to prevail when the animals are settling down to rest, and bodily contact occurs mainly when the animals are resting or when the young are nursing.

Within each of the two rodent types studied, one species (Microtus ochrogaster and Octodon degus) is believed, from earlier studies of adult social behaviour (Fitch, 1957; Getz, 1962; Krebs, 1970; Thomas and Birney, 1979; Madison, 1980; Fulk, 1976; Kleiman, 1974) to be more socially tolerant and communal than the other (Microtus pennsylvanicus and Octodontomys gliroides). Since behaviours involving contact account form a major part of the young rodent's behaviour repertoire, and thus early social

experience, it was predicted that differences between the more and less socially tolerant and communal species of each of the two rodent types would be found with respect to the amount of various contact behaviours between parents and young and among juveniles. The level of occurrence of these contact behaviours is described quantitatively for each individual species, and subsequently the species are compared in order to explore the extent to which these behaviours appear to be correlated with the type of social structure.

It is assumed that all the forms of contact discussed in this study relate in some way to inter-individual identification and attraction, and social relationships. Further, it is assumed that contact behaviours, particularly body sniffing and grooming, involve olfactory exchange. These assumptions are consistent with the conclusions of other authors. In the flying phalanger (Marsupalia: Petaurus breviceps) individuals exude odour from different body regions, and members of a community sniff one another with a predictable frequency that signifies a social 'association' between the individuals (Schulze-Westrum, 1969). Barnett (1963) has described body nosing in wild rats (Rattus norvegicus), and so also have Happold (1976 a, b) in four species of Australian conilurine rodents (Muridae), Kalkowski (1967; 1972) in laboratory mice, and Elliott (1978) in the eastern chipmunk (Tamias striatus), Sale (1970) in the rock hyrax (Dendrohyrax, Sp.), Müller-Schwarze (1971) in young black-tailed deer (Odocoileus hemionus columbianus), and Wilson and Kleiman (1974) in the harbour seal (Phoca vitulina

concolor), and Porter et al. (1978) in spiny mice (Acomys cahirinus). Stoddart (1974) reviewed some earlier literature on rats, mice and voles which points towards an olfactory basis for group cohesion. These authors have noted the prevalence of body nosing and other forms of body contact, and have considered these behaviours to contribute to individual identification and to promote social cohesion. It is likely, however, that the precise function of these behaviours may vary from species to species.

For the purpose of this study, young animals were observed in two principal contexts, i.e. in undisturbed family groups (together with their siblings and one or both parents) and in dyadic encounters with conspecifics of similar age. I chose to do most observations on each species in a context in which the most intense social activity was seen, and the context clearly differed in the two types of rodent. In voles, spontaneous activity periods of young in undisturbed family groups generated little social interaction and body nosing, whereas young voles in dyadic encounters engaged extensively in body nosing interactions and 'play' behaviours. By contrast, the caviomorphs in their home cages predictably engaged in vigorous social interaction which encompassed a wide range of body nosing behaviour patterns, including 'play', but in dyadic encounters their behaviour repertoire was reduced. Table 1.1 indicates the contexts in which I observed social behaviour for each of the four species. Generally, I recorded the juvenile interactions of voles in the dyadic encounter context, but the caviomorphs in the family group context. The less frequent observations during dyadic encounters in the caviomorph study is also due, in part, to the low reproduction rate and

Table 1.1. Differences in the observational emphasis and social conditions for the four rodent species studied.

	family groups			dyadic encounters	
	parent-young contact	parent-young nosing	sibling nosing	sibling	non-sibling
Microtus ochrogaster	++	+	+	++	++
Microtus pennsylvanicus	++	+	+	++	++
Octodon degus	++	++	++	+	0
Octodontomys gliroides	0	++	++	+	0

++ ... considerable emphasis + ... data included, but not emphasised

0 ... data not included

fewer available litters of these animals compared with the voles. Parent-young contact time for Octodontomys could not be included in the data since this species, unlike the other three, is strictly nocturnal and has a single peak of social activity at the onset of darkness, when observations were made.

The Microtus study is presented first (Chapters 2 and 3), followed by the caviomorph study (Chapters 4 and 5). In Chapter 2, the amount of parent-young contact in the two vole species is related to the species' social structure and adult contact-proneness described by other authors. In Chapter 3, the social behaviour of juvenile voles during dyadic encounters is described and compared in the two species, and then related to known characteristics of the species' social structure. Chapter 4 is devoted to a description of parent-young and sibling social behaviour in Octodon, including consideration of the role of the father in juvenile socialisation. In Chapter 5, the juvenile social behaviour of Octodontomys is compared with that of Octodon, and the comparison is discussed in terms of known and presumed aspects of social structure in the two species.

Chapters 2, 3 and 4 have been published in a form slightly modified from the presentation in this thesis (Wilson, 1982 a, b and c).

CHAPTER 2

PARENT-YOUNG CONTACT IN THE VOLES *MICROTUS OCHROGASTER* AND *MICROTUS PENNSYLVANICUS*

ABSTRACT

Two species of Microtus (M. ochrogaster and M. Pennsylvanicus) in captivity were observed in groups consisting of a litter and the mother. Observations were made daily in 15-min bouts and in 'spot checks'. The animals inhabited extensive runs of simulated runways, nest boxes and feeding areas. Observations focussed on the amount of mother-young contact. This measure declined with post-natal age in both species, but there was more mother-young contact in M. ochrogaster than in M. pennsylvanicus.

Some observations were also made of mated pairs with one litter. M. ochrogaster pairs spent more time together in contact with the young than did M. pennsylvanicus pairs; this measure did not decrease with post-natal age. M. ochrogaster fathers spent much time with the young while the mother was out of the nest; this time was highly correlated with maternal time away from the nest, although the correlation decreased with post-natal age. In M. pennsylvanicus, father-young contact time while the mother was out of the nest was only correlated with maternal time away during the first post-natal week. Mated mothers of both species gave birth again on post-natal d20-21; M. ochrogaster mothers remained in the same nest with the former litter, whereas maternal contact with the former litter decreased markedly towards the next birth in M. pennsylvanicus.

The results of this study are discussed with reference to other captive and field studies of parent-young contact in these species.

INTRODUCTION

Barnett (1963) speculated that the almost continuous stimulation experienced by infant rats from the mother might influence later huddling behaviour. Such a causal relationship has yet to be found, but Happold (1976b) found a correlation between the amount of social contact received by infants in the nest and later contact-proneness among different species of conilurine rodents (Muridae). Such a correlation may turn out to be widespread among mammals (Eisenberg, 1977).

The aim of the study described in this chapter was to test the hypothesis that infants of the prairie vole (Microtus ochrogaster) experience more body contact from their parents than do meadow vole (M. pennsylvanicus) infants, and that the amount of contact with parents as nestlings may be correlated with the degree of later contact-proneness in these two closely related species.

Previously published literature suggests that the prairie vole is a highly contact-prone species. Adult-sized individuals have been found huddling together in the field (Fitch, 1957) and mated pairs in captivity huddle closely together (Thomas and Birney, 1979). During adult dyadic encounters, adult prairie voles engage in much body contact and allogrooming when compared with meadow voles (Getz, 1962; Krebs, 1970), and I will show, in Chapter 3 of this thesis, that the same is true of weanlings of these two species. There is evidence from both captive and naturally occurring voles that prairie

voles tend to associate and breed in monogomous pairs, and that these pairs are intolerant of unfamiliar conspecifics (Thomas and Birney, 1979; Getz et al., 1981). Pair associations do not appear to occur in meadow voles under natural conditions (Madison, 1980; Getz et al., 1981). Circumstantial evidence for pair-bonding in prairie voles includes the refusal of a recently mated male to mate with a strange oestrous female in prairie voles, but not in meadow voles (Gray and Dewsbury, 1973), the necessity for a mated pair to cohabit for at least four days after mating to ensure pregnancy (Richmond and Stehn, 1976), and also the finding that pregnancy termination may be induced by a strange male up until at least the fifteenth day of pregnancy in prairie voles (Stehn and Richmond, 1975), but only in the pre-implantation stage in meadow voles (Clulow and Langford, 1971). Further, prairie vole families often include reproductively immature offspring from previous litters (Batzli et al., 1977; Thomas and Birney, 1979), and this is a characteristic feature of monogamy in mammals (Kleiman, 1977). By contrast, meadow vole mothers usually leave the litter and nest at weaning (Madison, 1978; 1980; 1981), and young apparently disperse shortly after the mother leaves (Getz, 1972). In the field, therefore, nestlings of the two species undoubtedly experience different social environments.

ANIMALS AND METHODS

Although a naturalistic social environment for the two species should differ on account of their contrasting social systems, such a simulation would not permit a quantitative behavioural comparison. Thus, the social environment was as similar and uncomplicated as possible for both species in this study. For observations of a mother and one litter, the male parent was removed from the family, and the mother not permitted to become pregnant again. Although probably rare for either species in the field, the elimination of the mate's presence and a subsequent pregnancy provided an opportunity for comparing species-specific tendencies for mother and young to make and maintain contact. Two-parent families were also observed in order to detect species differences in the contact contact time of males with mates and offspring; all mothers became pregnant during these observations. These results will only be summarised because of limited meadow vole data.

Prairie voles of the third or fourth generation in captivity were obtained from Dr M. Gaines, the original breeding stock having been captured in the vicinity of Lawrence, Kansas. Seven of these voles, and two generations bred from them, were the subjects of this study (and also of the study described in Chapter 3).

Although wild-caught prairie voles were unavailable since the study location was in Virginia, meadow voles from the field were available locally, and were used in preference to an available long-established breeding stock. Field-caught meadow voles are usually more difficult to breed in captivity than field-caught prairie voles (R. K. Rose, personal communication); this difference may derive from the relatively lesser social tolerance of meadow voles, or their strong adrenal response to capture (Olsen and Seabloom, 1973) - or both. Thus, use of meadow voles from a laboratory colony might have biased the results in favour of a socially tolerant type for which a laboratory colony would probably inadvertently select (Barnett and Stoddart, 1969).

The locally-caught meadow voles proved difficult to breed, but since live-trapped pregnant females successfully reared young in the observation enclosures, these mother-young units were the study subjects (Table 2.1). Eventually, two pairs, derived mainly from first generation young (Table 2.1), successfully bred, and these provided the limited data on meadow vole parent-young contact in the father's presence.

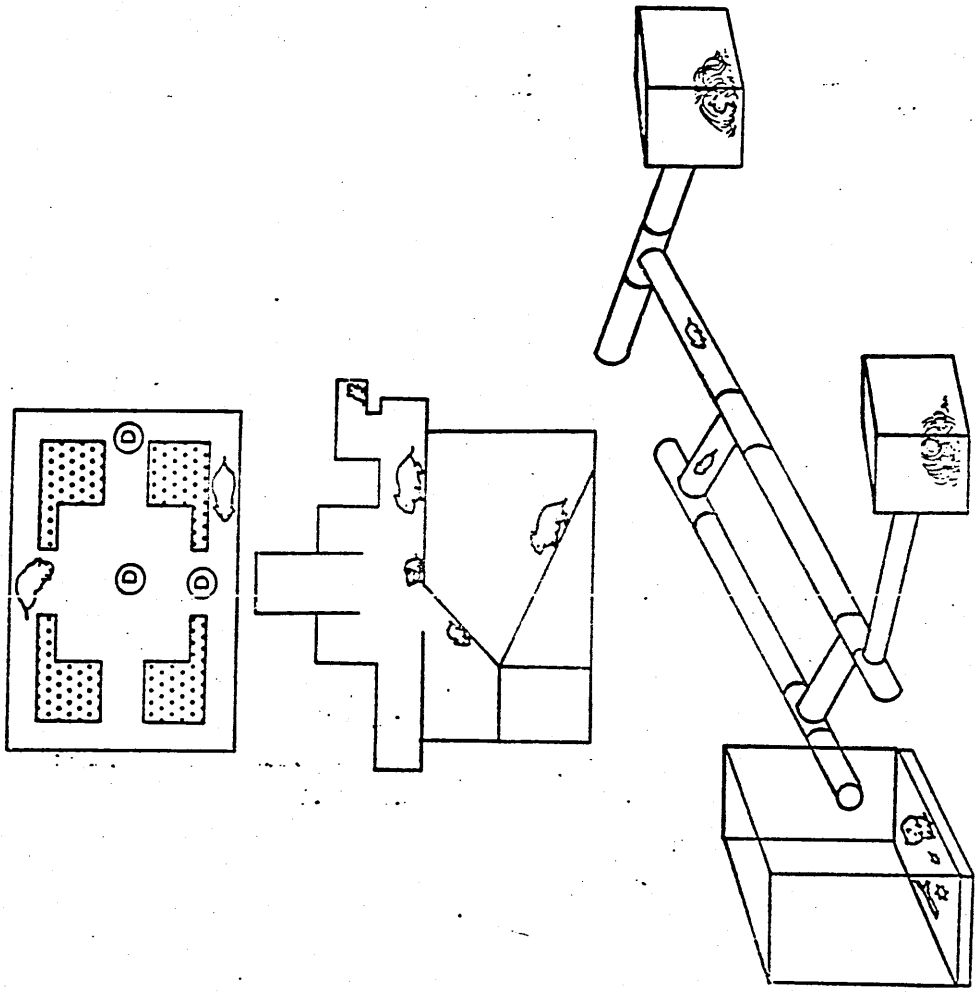
Observation enclosures were constructed of commercially marketed plastic units and formed networks of transparent plastic tunnels (Fig. 2.1). These units, although restrictive compared with

Table 2.1. Meadow vole units observed

Unit no.	origin of parents	type of enclosure (see Figure 1)	no. daily 15-min observations	no. days post-natal for which data used
father-absent units				
1	♀m Charlottesville, Va	c	2	21
2	♀p Charlottesville, Va	c	1	21
3	♀p Great Falls, Va	a-b	1	21
4	♀p Great Falls, Va	c	1	21
5	♀p Great Falls, Va	c	2	8
6	♀p Great Falls, Va	a-b	2	21
7	♀p Charlottesville, Va	c	2	21
8	♀p Great Falls, Va	c	2	9
father-present units				
9	♀m Patuxent, Md ♂ litter of unit 6	c	2	18
10	♀m litter of unit 6 ♂ litter of unit 8	a-b	2	18

m = mated in captivity; p = pregnant when captured

Figure 2.1. Observation enclosures. a-b. Hartz "hamster and gerbil castle" over a ten-gallon aquarium tank, one of the two types of enclosure used for observation. a - top view. Screw-on doors are indicated by D. Exterior dimensions are 53.5 by 35.5 cm; tunnels are 5.5 cm width and height. b - side view. The Hartz unit is linked to the tank below by a metal runway leading to the tank floor. c. A typical unit for family groups constructed from "Habitrail" sections. Each long length of tunnel measured 35 cm. This was the second type of enclosure used for observations.



a b c

the field condition, provided the animals with opportunities to move and nest separately, thus permitting species differences in the amount of parent-young contact to be expressed. Two types of observation enclosure were used (Fig. 2.1; Table 2.1). Nesting material of surgical cotton, hay and grass was provided; wood shavings were used as a substrate. The animals had constant access to water and a dry-food mixture of nuts, seeds and rabbit chow; fruit and vegetables were given daily, and fresh grass was given when available. The enclosures were in a basement room which was dimly illuminated naturally in the daytime and by electric light in the evening. The room was usually in darkness for five to seven hours at night, and was maintained between 50 and 70 F according to the season and time of day.

The behaviour of mother-litters groups was observed daily in observation bouts of 15 minutes duration for 21 days post-partum. Nine prairie vole mother-litter units, including six different mothers, were observed once daily at an arbitrarily chosen time during the light phase of the daily cycle. Eight different meadow vole mothers with one litter each were observed similarly, although five of the eight units were observed twice daily, with at least two and a half hours between each observation. For each 15-min observation the total time the mother spent in continuous bodily contact with at least one infant and the number of body nosing contacts between mother and young and among littermates outside the nest were recorded. 'Spot checks' were also made daily on each mother-litter unit, with at least two and a half hours between each check. The number of young in the litter (1) in bodily contact with the mother and (2) resting without the mother, were recorded at each check.

The two and a half hour minimal interval between 15-min observations and spot checks was based on the assumption that many small rodent short term activity cycles have a periodicity of about two hours (Ashby, 1972); however, lactating voles may in fact have a longer cycle than this, since Madison (1981) found that the activity period of lactating meadow voles in the field declined from 6.5 h on post-natal day 2 to 4.0 h on day 12.

RESULTS

Since the family groups were observed at arbitrarily chosen times of the day, the amount of parent-young contact in a 15-min observation period ranged from 0 - 15 minutes, depending partly on the phase of the activity cycle sampled and partly on the age of the young. The purpose of this type of data collection was to obtain a sufficiently large number of observation samples covering a number of different families at all phases of the activity cycle and arrive at estimates of the average amount of parent-young contact per 15-min period occurring at any given post-partum age of the young up to three weeks of age. The data are therefore highly

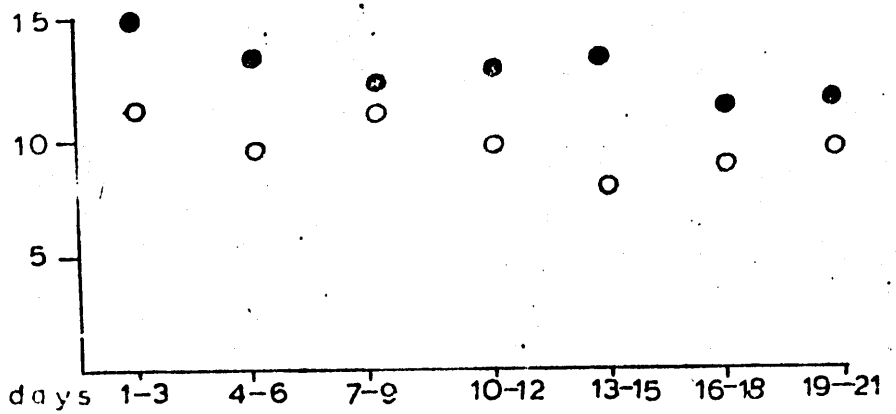
skewed, rendering standard measures of variance and presentation of scatter inappropriate. Fig. 2.2 presents the mean times of mother-young contact for each species at different ages. The means are presented here for illustrative purposes because of the progressive nature of the changes with age, although a non-parametric test (The Kolmogorov-Smirnov 2-sample test; Siegel, 1956) was used to compare the species at different ages on account of the skewed data distribution. In the Kolmogorov-Smirnov test, the contact time (to the nearest minute) for each 15-min observation period was used singly in comparison of the magnitude and variance of contact times for each species.

In accordance with the hypothesis, prairie vole mothers were found to spend more time in bodily contact with their young than were meadow vole mothers (Fig. 2.2). The one-tailed significance of this difference was assessed for the first post-natal three-day period and subsequent six-day periods by the Kolmogorov-Smirnov test (Fig. 2.2), with each 15-min observation period being divided into 15 one-min segments. The spot-check data pooled from all mother-litter units of each species similarly indicated that meadow vole infants rested more often alone and less often with their mother than did prairie vole infants (one-tailed $P = 0.008$, Sign test, comparing the data for each species for each three-day period; Fig. 2.3). In conjunction with these results it was noted that prairie vole but not meadow vole young attach tightly to the mother's nipples; to leave the nest, the mother must usually pluck each infant from the nipple.

A regression analysis on mean mother-young contact time for each three-day period indicated a significant linear decline with

Figure 2.2. Time spent by mothers in contact with young.

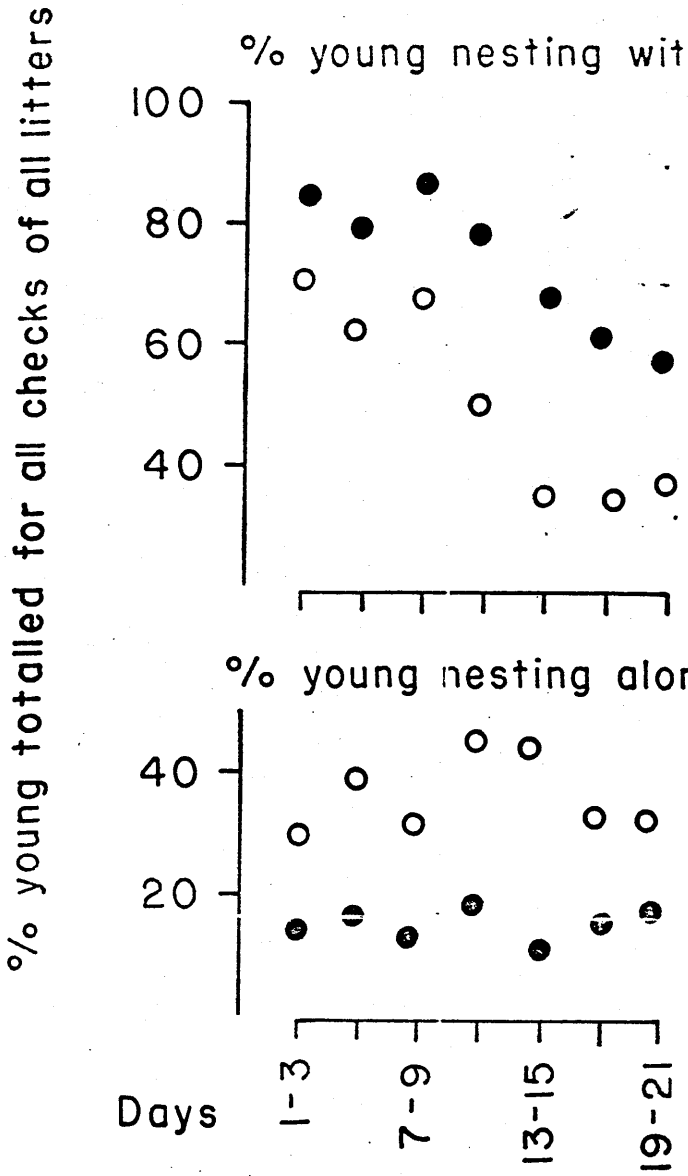
● M. ochrogaster; o M. pennsylvanicus. Ordinate is time per 15 min mother was in contact with at least one infant.



n 15 min. obs.							
M. ochrogaster	19	24	24	24	24	24	23
M. pennsylvanicus	39	39	39	27	27	27	27
χ^2	8.55	9.06		17.08		10.35	Kolmogorov-Smirnov
P	<.02	<.02		<.001		<.01	2-sample test

Figure 2.3. State of young observed in spot checks.

● M. ochrogaster; o M. pennsylvanicus



n (young from 9 litters of M. ochrogaster)

531 630 619 637 601 542 514

n (young from 8 litters of M. pennsylvanicus)

551 535 512 418 406 355 301

post-natal age for both species (for prairie voles the slope of the regression line, b, = -0.16; correlation coefficient, $\underline{r}$, = -0.82, one-tailed $\underline{P} < 0.005$; for meadow voles b = -0.14; $\underline{r}$ = -0.68, $\underline{P} < 0.05$).

For both species, the frequency of body nosing contacts by the young to the mother increased from day 8 to the third week of age from 0.0 to between 0.5 - 1.0 contacts per young per 15 min. The mean frequency of mother-to-young nosing contacts had a similar ontogeny, but was always fewer than for contacts from young to mother when three-day means were considered from post-natal day 10 to 21.

To ensure that the different enclosures used in this study (Fig. 2.1; Table 2.1) did not affect the results, mother-young contact in the two main types of enclosure was compared for days 4-9 and 16-21 by the Kruskal-Wallis analysis of variance. There was no significant influence of the enclosure type on mother-young contact time in either species (four prairie vole mother-litter units in each enclosure type; $\underline{P}$ = 0.90 for d 4-9 and 0.20-0.30 for d 16-21; for meadow voles, units 3 and 6 were compared with units 2, 4 and 7 (Table 2.1); $\underline{P}$ = 0.10-0.20 for d 4-9 and $\underline{P}$ = 0.30-0.50 for d 16-21).

Fifteen-min observations were also made once daily on five different mated pairs of prairie voles, each with two different litters, and twice daily on two different meadow vole pairs with one litter each (Table 2.1).

Prairie vole pairs spent more time together in the nest with at least one infant (mean time per 15-min = 8.3 min; n = 205 15-min observation periods between days 1-21; during only

20% of observations did the pair spend no time together with the young) than did the meadow vole pairs (mean time = 2.5 min; n = 76 observations between days 1-20; during 51% of observations the pair spent no time together with the young). Neither species showed any change in this measure with post-natal age, and the species difference was consistent, considered in three-day periods, throughout the three weeks of observation (one-tailed $\underline{P} = 0.008$; Sign test).

Prairie vole males usually sat with the young while the mother was absent from the nest. Paternal sitting time was almost equal in duration to, and highly correlated with, maternal time off the young during the first post-natal week (b, the regression line slope, = 0.97; n = 19 15-min observations during which there was some maternal time off the young; $\underline{r} = 0.87$, $\underline{P} < 0.01$). However, the correlation decreased in the second week (b = 0.44; n = 31; $\underline{r} = 0.50$, $\underline{P} < 0.01$) and still more in the third week (b = 0.37; n = 37; r = 0.32, P = 0.05). There was a linear, but only slight, decline with age in mother-young contact time, from a mean of 12.23 min per 15-min on d 1-3 to 10.86 on d 19-21 (b = -0.10; $\underline{r} = -0.76$, $\underline{P} \leq 0.01$). All the mothers gave birth again when the young were three weeks of age. No significant differences were found (by the Kolmogorov-Smirnov two-sample test) in mother young contact time between the father-present and father-absent groups at any post-natal age.

Paternal sitting time for meadow voles with the young in the nest was shorter than maternal time out of the nest, and was correlated with the latter measure during the first post-natal week (b = 0.69; n = 19; $\underline{r} = 0.58$, $\underline{P} < 0.005$) although not during the second week (b = 0.2; n = 22; $\underline{r} = 0.14$, $\underline{P} > 0.10$). There was a decline with

age in mother-young contact time, from a mean of 11.17 min per 15-min on d 1-3 to 6.10 min on d 16-18 ($b = -0.28$; $\underline{r} = 0.72$, $\underline{P} < 0.05$). For the one family unit observed during days 19-21, contact between mother and young ceased abruptly after day 18; the mother made a new nest which she occupied alone, and in which she gave birth to a new litter on d 21. The small sample size precludes comparing the mother-young contact-time for the father-present and father-absent units. However, mother-young contact time was similar for both groups for d 1-3 ($\overline{X} = 11.43$ for father-absent, and 11.17 for father-present), but thereafter the rate of decline was greater for the father-present group.

In the father-present meadow vole units one mother was wild-caught and the other captive-born (Table 2.1), but there was no significant difference between them in the amount of time they spent with the young ($\underline{P} = 0.5$-0.7 for d 4-9; $\underline{P} = 0.1$-0.2 for d 10-18 by the Kruskal-Wallis analysis of variance) or in the amount of time they spent together with the mate and young ($\underline{P} = 0.1$-0.2 for d 4-9 and 0.95-98 for d 10-18).

DISCUSSION

Thus the hypothesis, that prairie vole nestlings experience more bodily contact from their parents than do meadow vole nestlings was supported. A species difference in mother-young contact time was evident in isolated mother-litter units where the mother was

not pregnant during lactation. Although a linear decline in mother-young contact with post-natal age was found for mother-litter units of both species, the decline was slight, and did not accelerate as the young became nutritionally independent during the third week of age.

Since the mother and young could nest separately, continued mother-young contact through the third post-natal week may reflect the essentially social nature of reproductively inactive or sexually immature voles of both species. Although prairie and meadow voles may both be contact-prone, there is a difference of degree; for the prairie vole such sociality is more expected within the extended family group (Batzli et al., 1977; Getz et al., 1981).

Hartung and Dewsbury (1979) have queried the validity of comparative studies of paternal behaviour of small rodents in captivity, since they noted considerable father-young contact in six rodent species studied in laboratory cages, and they were unable to distinguish contact time between father and young from that between mother and young in most species, regardless of presumed social organisation. Since the male meadow vole probably does not nest with the female and young in nature, Hartung and Dewsbury doubt the validity of such captive observations. However, although both Hartung and Dewsbury and I found that adult male meadow and prairie voles are tolerant of nestlings when confined with them, we also found that prairie vole males spend more time with the young than do meadow vole males.

Additionally I found that prairie vole males spend more time than do meadow vole males in the nest while the mother is with the young, and also spend a greater proportion of the mother's absentee time with the young. Prairie vole fathers have been observed taking young from the mother and squatting over them; such enthusiasm for nestlings was not observed in meadow vole males. Thus, there is a detectable difference between the species in father-young and mother-young contact in captive conditions, and the magnitude of this difference may be all that is necessary for a major species difference in social structure to be perpetuated in natural conditions, i.e. pair-bonding and a cohesive extended family group in prairie voles versus independent nests and home ranges of mated meadow voles (Getz et al., 1981; Madison, 1978; 1980). If captive meadow vole parents spend a limited time together in the nest, it does not mean that such nest sharing necessarily occurs in the field: these captive observations may only reflect the male's social tolerance of conspecifics, the relatively confined conditions of the enclosure, and the absence of other classes of conspecific with which the male might otherwise make contact (Getz, 1972). My results also do not necessarily suggest for either species that the father's presence contributes to the growth and survival of the young as in Peromyscus californicus (Dudley, 1974), although some influence of the father on the development of social responsiveness and perhaps later sexual preferences of the young might be predicted in view of the continual non-aggressive contact observed between father and young, and hence continual exposure of the young to the odours of the breeding male. Such an influence would probably be greater, in terms of nestling exposure to the male, in prairie voles than in meadow voles.

Comparison of the results of this study on mother-young contact in meadow voles with those obtained from the field by Madison (1981) may help to assess the validity of this and other captive studies. Madison's data indicate that mothers spend about 62% of total time with their young on day two, compared with about 75% of time on days 1-3 in my study (in both father-present and father-absent groups). In Madison's study the time had decreased to 50% by day 12. In the two father-present units of the present study the time had decreased to 47% by days 7-9, but in the father-absent group it decreased only to 73% by days 7-9 and thereafter to 58%. This comparison suggests that mother-young contact time in captive meadow voles may be slightly enhanced in the neonatal period, but is otherwise roughly comparable to the field situation. As expected, the father-present units (in which post-partum matings occurred) resembled the field condition in terms of the post-partum decline in mother-young contact more closely than did the father-absent units. This distinction is not relevant for prairie voles (for which there are no field data on mother-young contact) since there was no difference in mother-young contact between the father-present and father-absent groups.

To conclude, the results of this captive study on parent-young contact time in prairie and meadow voles are consistent with predictions made from field and other laboratory studies, and should be encouraging to further comparative studies of parental behaviour of small rodents in captivity.

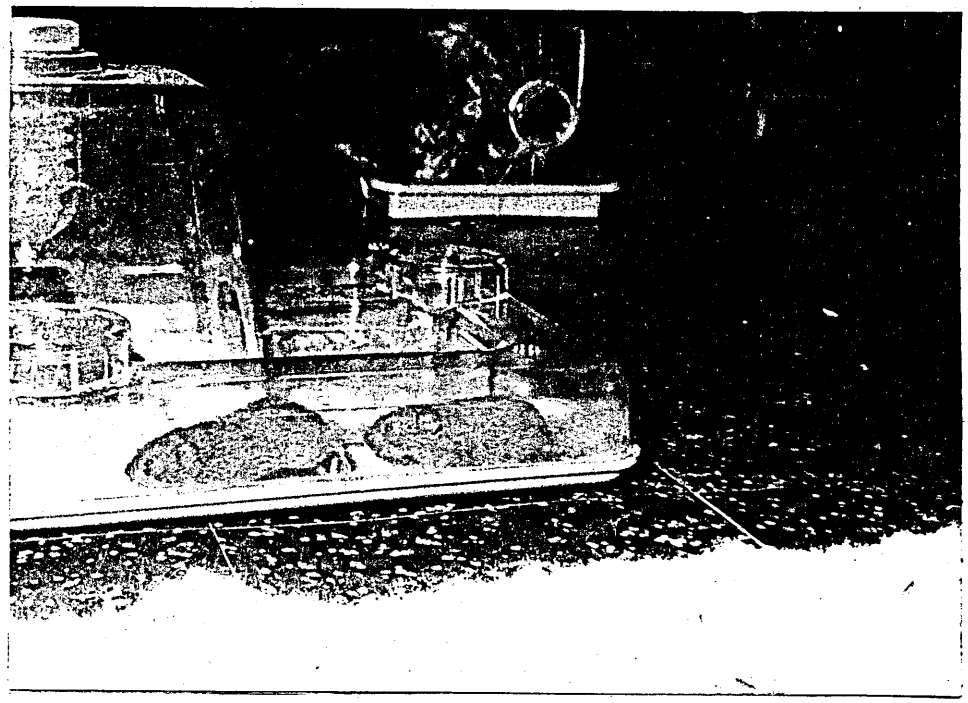
CHAPTER 3

THE DEVELOPMENT OF SOCIAL BEHAVIOUR BETWEEN SIBLINGS AND NON-SIBLINGS OF THE VOLES *MICROTUS OCHROGASTER* AND *MICROTUS PENNSYLVANICUS*.

FRONTESPIECE

Two *M. ochrogaster* in the dyadic encounter enclosure

One half of the enclosure is shown in the foreground. The two voles are 24-day old siblings. One is running away from the other after a Mode II interaction; the vole on the right is displaying the relaxed open mouth, typical of Mode II interactions.



ABSTRACT

It has been suggested that the amount of contact-promoting behaviour between young voles during the juvenile period may influence the species' social structure. Two Microtus species with contrasting social systems, M. ochrogaster and M. pennsylvanicus, were chosen for a comparative study of juvenile social behaviour. Young were observed in sibling and non-sibling dyadic encounters from the second until the seventh week of age. Social interactions consisted mainly of body nosing of the partner, and included behaviours interpreted as investigation, socialisation and settling. Only minor sex differences in body nosing scores occurred, but some ontogenetic trends were noted. When the species were compared, M. ochrogaster received higher scores for body nosing and sitting in contact, and displayed more reciprocity in their nosing, than did M. pennsylvanicus, whether siblings or non-siblings were considered. When the sibling types were compared, non-sibling dyads received higher nosing scores than did siblings in both species, but the disparity was greater in M. ochrogaster then in M. pennsylvanicus. These results are interpreted with reference to known behavioural and developmental correlates of the extended family system in naturally occurring M. ochrogaster and the less communal social system in M. pennsylvanicus.

INTRODUCTION

The aim of this chapter is to describe the natural social behaviour of juvenile prairie voles (M. ochrogaster) and meadow voles (M. pennsylvanicus) in dyadic encounters between young of the same age, to quantify species differences in the performance of various components of the juvenile social behaviour repertoire, and to chart the ontogeny of these components.

Juvenile voles make contact with each other by huddling together during periods of inactivity, and by approaching and gently nosing one another's bodies during activity periods. I have briefly described the body nosing behaviour in an earlier paper on another Microtus species, M. agrestis (Wilson, 1973): juveniles in sibling groups repeatedly nosed one another gently in the snout, neck and rump regions during activity periods. Huddling together and repeated body nosing exchanges appear to dominate the social life of young voles with other family members, and are probably, therefore, influential in the creation and maintenance of social structure. By quantifying this behaviour during juvenile development in prairie and meadow voles, I hoped to correlate the differences in juvenile social behaviour in these two closely related species with differences in the species' social systems.

Previously published literature (summarised in the Introduction to Chapter 2) suggests that adult prairie voles are more contact-prone than meadow voles, that prairie voles show a strong tendency towards pair-bonding, whereas meadow vole males are not thought to share a nest with their mates. In addition prairie voles

tend to live in extended family groups including reproductively inactive grown young, whereas the meadow vole mother-litter unit is believed to last only until weaning. In Chapter 2, I presented some data indicating a greater amount of contact between nestlings and both their parents in the prairie vole than in the meadow vole.

It is usual for both prairie and meadow vole young to have two or more siblings. Litter size averaged more than four young for both species during my study, and also in the prairie vole study of Kruckenberg et al. (1973). At 9-10 days of age, the young of both species emerge from the nest for the first time (Pépin and Baron, 1978; see also Chapter 2). Meadow vole young in the field are thought to disperse from their natal site gradually during the first 10 days after weaning, which occurs by the beginning of the third week of age (Getz, 1972). At this time the mother withdraws to a new nest site (Madison, 1978). Thus meadow vole siblings may remain in the company of each other for about two weeks after they first emerge from the nest. During this two-week period, however, they may also encounter neighbouring conspecifics, probably without aggression (Getz, 1972). Intralitter social bonds therefore probably become complicated, from about two weeks of age, by social ties which may develop between young and unrelated neighbours.

Prairie vole young in natural populations probably have a longer opportunity than meadow vole young to enjoy relations with parents and siblings uncomplicated by social ties developing with unrelated neighbours. Prairie vole young are not thought to

disperse upon weaning, but to remain with the parents at least through birth and weaning of the next litter. An extended family living in a well-defined home range may develop (Fitch, 1957; Batzli et al., 1977; Thomas and Birney, 1979). Thus young prairie voles may be expected to interact almost exclusively with parents and siblings for at least four to five weeks after their first emergence from the nest.

The prairie vole situation, therefore, is one in which the degree of familiarity between juveniles is close to their degree of relatedness (Bekoff, 1981). From the foregoing discussion, it is evident that the degree of familiarity between meadow vole young may not necessarily reflect their relatedness after about three weeks of age. Since the prairie vole situation, in contrast to that of the meadow vole, appears to provide highly favourable conditions for promoting sibling interactions, I predicted that juvenile prairie vole siblings would engage in more huddling and body nosing contacts than would their meadow vole counterparts during dyadic encounters. I also predicted that prairie vole young would differentiate clearly in their social behaviour between siblings and non-siblings when compared with meadow vole young. This study tests these predictions. Within the framework of the above discussion, the sex and age of young voles has not been attributed any importance. However, the possibility that these factors may influence juvenile social behaviour has been investigated.

ANIMALS AND METHODS

Source of animals and colony maintenance

Prairie voles of the third or fourth generation in captivity were obtained from Dr M. Gaines, the original breeding stock having been captured in the vicinity of Lawrence, Kansas. Thirty litters bred from an original seven voles and their offspring were used for dyadic encounters.

Meadow voles were trapped near Charlottesville in Virginia, Great Falls in northern Virginia, and Mount Desert Island in Maine. Most of the young used in this study were from 18 captive-born litters of first or second generation of offspring of live-trapped voles. However, since more animals were needed, an additional 42 young were live-trapped from the above locations. Nine of these young may have been siblings (judging from the location and time of capture, and similarity in size and state of moult); they were therefore housed with one another and treated as siblings. The age of live-trapped young at capture was estimated from their size and state of moult in comparison with captive-born young. 30% of the total meadow-vole non-sibling encounters used two wild-caught young, and a further 20.8% used one wild-caught and one lab-reared young. Only 5.5% of meadow vole sibling encounters used wild-caught young.

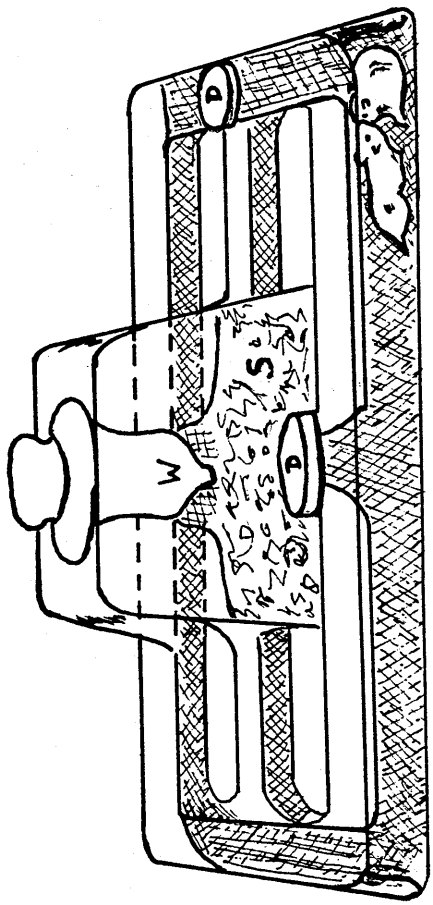
Voles were maintained in sibling groups after weaning, in holding cages ranging in size from standard laboratory rat cages to wooden or metal cages measuring 100 x 60 x 50 cm. The larger cages were used preferentially. The substrate was wood

shavings, pine mulch or peat moss; hay, grass and surgical cotton were liberally supplied. The cages were kept in a basement room which was dimly illuminated naturally in the daytime and by electric light in the evening. The room was usually in darkness for five to seven hours at night, and was maintained between 50 and 70 F, according to the season and time of day. Dry food (a mixture of seeds, grains, nuts and rabbit chow) was fed daily and supplemented daily with fresh fruit and vegetables, and also meadow grass when available. Water was always available. Twigs and wooden blocks were given for gnawing.

Dyadic encounter enclosure

The encounter enclosure was rectangular in shape, measured 53.5 x 35.5 cm, and consisted of an outer transparent tunnel (5.5 cm width and height) with a tunnel connecting at right angles from each side to an open central area (Fig. 3.1). The floor was a sheet of plastic to which the upper part, moulded into the tunnel walls and roof, clipped on (this unit is marketed commercially in the U.S. as the Hartz 'hamster and gerbil castle'). Wood shavings and a little nut and seed mix were scattered over the floor of the central area, and a water bottle hung through the roof. Voles were introduced into the enclosure through either of two removable doors in the roof.

Figure 3.1. The dyadic encounter enclosure. S = wood shavings, W = water bottle, D = removeable doors.


D
W
S
D

Design of observations

The social behaviour of juvenile dyads in the encounter enclosure was observed in weekly stages from the second to the seventh week of age. Encounters were carried out in the same room as the holding cages at arbitrarily chosen times during the light phase of the daily cycle.

Each encounter was classed into one of six weekly intervals. For each age class, encounters were further divided into sibling and non-sibling dyads, although non-sibling encounters did not commence until the third week of age. Each sibling type was further divided into ♂♂, ♂♀ and ♀♀ classes. Ten encounters involving 20 different individuals were achieved for almost all species/sibling/age/sex classes; exceptions were meadow vole non-sibling ♀♀ at three and four weeks of age (only six and seven respectively) and sibling ♀♀ at seven weeks of age (only nine). Since non-siblings of the same age were not always available, a week's difference in age for a dyad was permitted; such an encounter was classed with the age of the elder animal. Littermates were distinguished by fur clipping.

Procedure for recording encounters

Behaviour was normally recorded for 15 minutes starting with the entry into the enclosure of the second vole. This is five and ten minutes longer than the recording times used by Krebs (1970) and Getz (1962) respectively. The 15-min period was considered necessary for most dyads to complete their initial

intensive investigation of one another and begin 'settling' behaviours, such as huddling and social grooming.

If the voles interacted within the first five minutes after entry, the normal procedure of recording behaviour for 15 minutes was followed. However, several meadow vole dyads displayed long interaction latencies during which they often sat quite immobile or moved hesitantly and jerkily. When these animals were disturbed by me at the end of the encounter, they often accidentally contacted each other and then proceeded to engage in mutual body nosing without hesitation. It seemed, therefore, that at least some of these long meadow vole interaction latencies were an artifact of the encounter procedure. In an attempt to overcome this problem, the following procedure was adopted with dyads displaying long interaction latencies. If interaction was initiated during the first 30 minutes, 15 minutes were recorded starting from the first whole minute after entry in which they first interacted. The actual interaction latencies were analysed separately from social behaviours recorded during the 15-min period. However, if the voles did not interact within 30 minutes, the trial was discarded from all analyses.

A narrative of the behaviour of both animals was written as observed, using a behaviour code. A time check throughout the encounter was kept, using a stop watch. The behavioural record for each encounter was later transferred to a check sheet in which the encounter was divided into 15 1-min intervals, and the behavioural record for each member of the dyad was separated. These 1-min divisions facilitated one-zero scoring for continuous behaviours

(sitting in contact, autogrooming and eating; see section on behaviour measurement for explanation of one-zero scoring), and provided the time frame for an analysis of behavioural trends from the start to end of encounters.

After each encounter the voles were removed by unclipping the upper part of the enclosure from the floor. Faecal pellets were removed and urine marks were cleaned with a sponge. However, the woodshavings and scattered dry food in the enclosure were not changed between encounters of the same species, in order to create a background ambience of 'vole'.

Social behaviour recorded

Social behaviour observed consisted mainly of the voles nosing one another's bodies in a gentle and unhurried manner, and engaging in mutual body contact involving much of the body surface. This behaviour will be referred to as 'amicable' social contact. Behaviour was considered 'defensive' when a vole responded to another's approach by boxing with the forepaws in a jerky manner, squeaking audibly, or lunging. Chase, attack and sexual behaviours were not observed.

Amicable social contact included the following components:

Body nosing One animal's nose touches the other's body while sitting together, moving around one another, approaching, following, or passing one another. Nosing contacts were directed at the snout, neck, rump and anogenital regions. Body nosing sometimes occurred in the partial or complete mutual-upright or supine-quadrupedal positions (Fig. 3.2).

Allogrooming One vole nibbles the fur or skin of the other.

Figure 3.2

Examples of Mode I body nosing between juvenile Microtus

a Positions for nose-to-snout contact

b Positions for neck nosing

c Positions for anogenital and rump nosing

All sketches are from photographs, mainly of M. ochrogaster

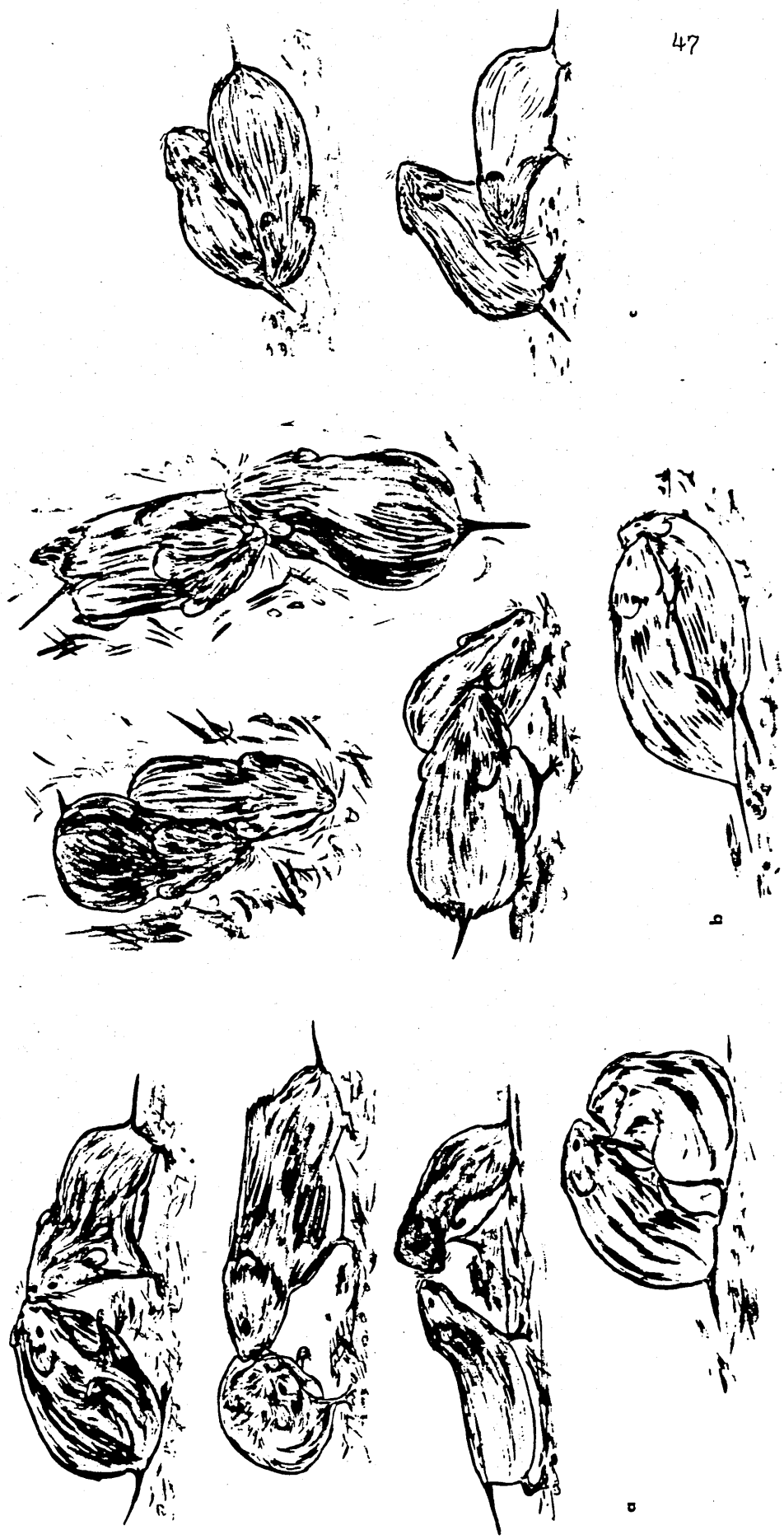


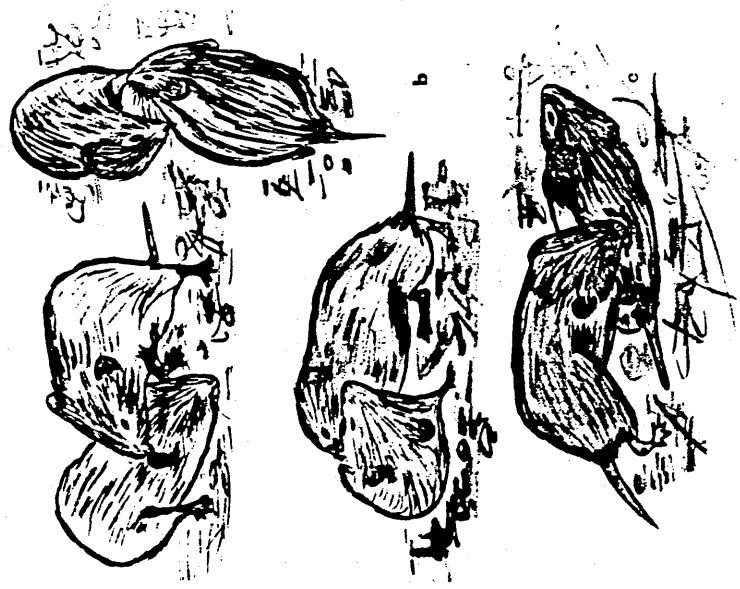
Figure 3.2 contd.

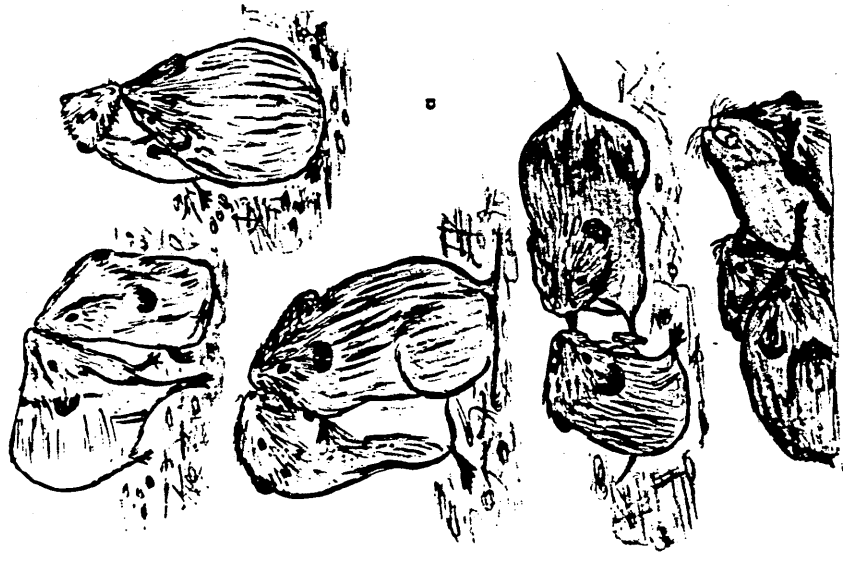
Examples of Mode II body nosing between juvenile Microtus

a Positions for nose-to-snout contact. In the second, third and fourth sketches from the top, the voles are partially or fully in the mutual-upright position. In the bottom sketch the vole on the right has just tumbled backwards after contact with the vole in the centre.

b Positions for nose-to-neck and nose-to-rump contact. In the top right sketch the voles are in position for reciprocal neck nosing with head rocking. In the third and fourth sketches the voles are partially in the supine-quadrupedal position.

All sketches are from photographs of M. ochrogaster





Rotational movement A vole rocks its head while nosing the other's body, or breaks nose-to-body contact with a head shake.

Sitting in contact The voles sit side by side, in physical contact. Alternatively, one may huddle over the other's back.

Two distinct modes of body nosing were observed. The most common (Mode I) involved unilateral or mutual body nosing in bouts of one, a few, or many nosing contacts. In the less common mode (Mode II), body nosing was accompanied by rotational head movement or extremely rapid manoeuvering by the animals as they changed body nosing positions. Other behavioural characteristics sometimes accompanied Mode II body nosing: rapid repetition of body nosing, partial or complete adoption of the mutual-upright or supine-quadrupedal positions with the mouth held slightly open, and retrieval of a departing partner by gentle gripping of the loose skin of the rump or neck. Anogenital nosing did not occur. Mode II behaviour probably corresponds to that which has been called 'play' by myself and other investigators (Wilson, 1973; Wilson and Kleiman, 1974; Fagen, 1981). A Mode II interaction is defined in this paper as an interaction, from the voles' approach until their separation, which involves some Mode II behaviour.

Behaviour measurement

Measurement of body nosing contacts was based on the fact that most body nosing contacts were instantaneous. Each contact normally received a 'body nosing score' of one, classed with the nosing animal and the body target nosed. However, the score was adjusted for nosing contacts which were measureably longer than

an instant (i.e. ca. 2 sec and longer), including all instances of allogrooming: these received a body nosing score of two (arbitrary weightings). Nose-to-snout contacts were not scored for each individual, but only for the dyad jointly.

Allogrooming, Mode II behaviour, and defensive behaviour were also measured in terms of a 'behaviour act score'. Each performance of such a motor pattern by each animal received a score of one act. However, defensive squeaking, boxing and lunging could occur simultaneously in one individual, and only one act would then be scored. Similarly, simultaneous Mode II acts by one animal received only a collective score of one act. Since Mode II behaviour tended to be episodic, the distribution of this behaviour according to species/sibling/age/sex classes is described in terms of Mode II interactions (see above definition) rather than of Mode II behaviour acts.

Continuous behaviours, i.e. sitting in contact, autogrooming and eating, were scored according to whether or not they occurred during each of 15 1-min intervals (the 'one-zero' method; Altmann, 1974). For sitting in contact by the dyad, the maximum score per encounter was 15. Since both members of the dyad could autogroom and eat independently of each other, the maximum score per encounter for each of these behaviours was 30.

RESULTS

Behaviour from start to end of encounters

The trends in behaviour scores from the start to end of encounters were assessed by a regression analysis on the mean scores for different behaviours in each successive 3-min period of the encounter for all encounters in each species/sibling class.

Snout, neck and rump nosing occurred maximally at the start of encounters and progressively declined by the end. The correlation coefficients (r) with time ranged from -0.77 to -0.92 (1-tailed $P<0.05$) for each species/sibling class. Anogenital nosing by prairie vole non-siblings also showed a progressive decline from start to end ($r = -0.91$, $P < 0.01$), but insufficient anogenital nosing occurred with the other species/sibling classes for any trend to be detected. Autogrooming declined during the encounter, as did defensive acts by non-siblings of both species (r ranged from -0.75 to -0.99; $P < 0.05$); siblings of both species engaged in virtually no defensive behaviour. These behaviours (body nosing, autogrooming and defensive manoeuvres) were temporally associated with social investigation.

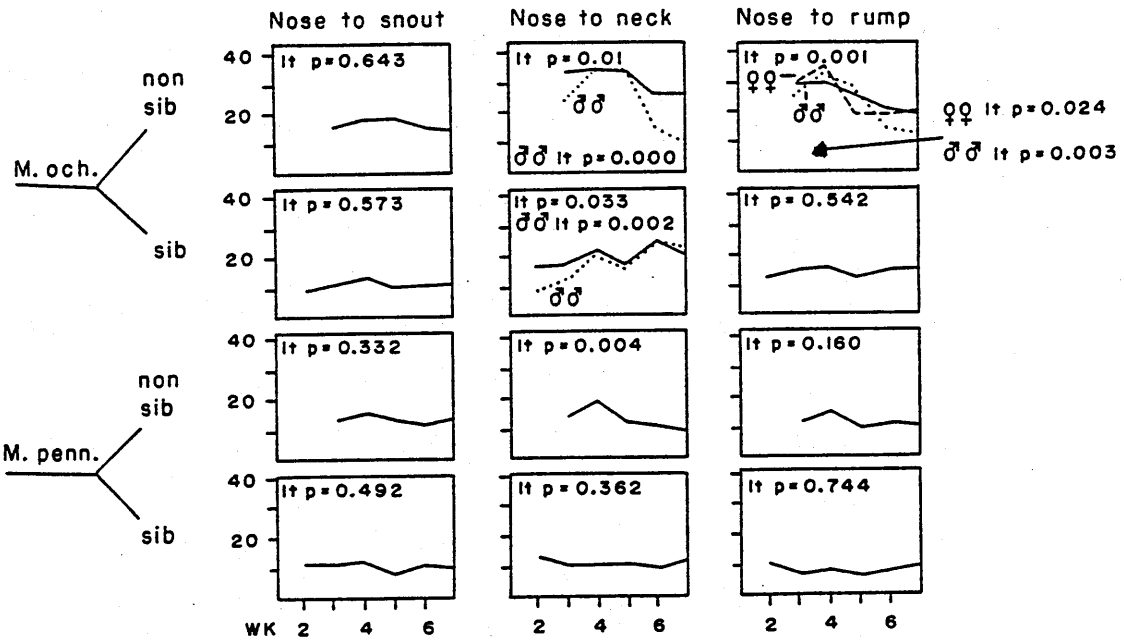
Sitting in contact, eating and allogrooming all tended to increase throughout the encounter (r ranged from 0.73 to 0.94, $P < 0.05$ for prairie voles only; meadow voles did insufficient autogrooming for a trend to be detected). I interpreted these behaviours as being associated with settling, i.e. increasing stability of the dyadic relationship. Mode II acts showed some tendency to increase from start to end of encounters, but r was only significant at the 5% level for meadow vole siblings and prairie vole non-siblings.

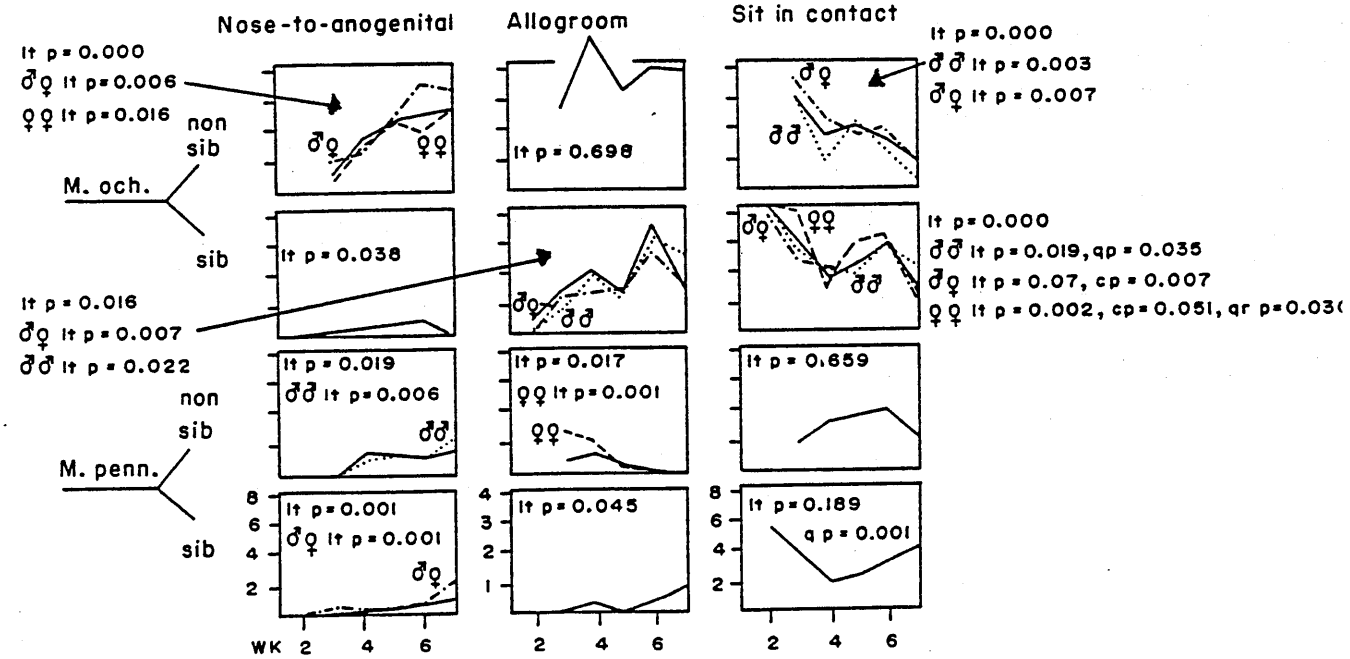
The ontogeny of social behaviour

Mean scores for body nosing, allogrooming and sitting in contact are presented in Fig. 3.3 for each species/sibling/age class. Ontogenetic trends in these scores were tested for significance using a trend analysis (Ferguson, 1966). The sex classes were not graphed separately except where a significant ontogenetic trend was found for a particular sex class (Fig. 3.3).

Scores for nose-to-snout contact remained constant with age in both species. Nose-to-neck contact scores between non-siblings decreased with age in both species; the decrease was most marked for prairie vole non-sibling males in the sixth and seventh weeks. Between siblings, nose-to-neck contact increased with age in prairie voles and remained constant in meadow voles. Nose-to-rump contact decreased with age between non-sibling prairie voles; the decrease was especially marked for ♂♂ and ♀♀ dyads. Rump nosing scores did not change with age in the other species/sibling classes. Anogenital nosing increased with age in both sibling classes of both species; the increase was most marked for prairie vole non-sibling ♂♀ dyads. Allogrooming between siblings increased with age in both species; with non-sibling meadow voles it decreased with age. Scores for sitting in contact decreased with age in prairie voles, but not in meadow voles; however, with siblings

Fig. 3.3. Ontogenetic trends in behaviour scores.
♂♂ .....; ♂♀ .-.-.; ♀♀ - - - ; combined sex classes -------; lt = linear term; q = quadratic term; c = cubic term; qr = quartic term.
P values are given to three decimal places.


Nose to snout
Nose to neck
Nose to rump
non sib
M. och.
sib
non sib
M. penn.
sib
lt p=0.643
lt p=0.01
♂♂ lt p=0.000
lt p=0.001
♀♀
♂♂
♀♀ lt p=0.024
♂♂ lt p=0.003
lt p=0.573
lt p=0.033
♂♂ lt p=0.002
lt p=0.542
lt p=0.332
lt p=0.004
lt p=0.160
lt p=0.492
lt p=0.362
lt p=0.744
40
20
WK 2 4 6


Nose-to-anogenital
Allogroom
Sit in contact
lt p=0.000
♂♀ lt p=0.006
♀♀ lt p=0.016
non sib
M. och.
sib
lt p=0.698
lt p=0.000
♂♂ lt p=0.003
♂♀ lt p=0.007
lt p=0.038
lt p=0.016
♂♀ lt p=0.007
♂♂ lt p=0.022
lt p=0.000
♂♂ lt p=0.019, qp=0.035
♂♀ lt p=0.07, cp=0.007
♀♀ lt p=0.002, cp=0.051, qr p=0.03
lt p=0.019
♂♂ lt p=0.006
lt p=0.017
♀♀ lt p=0.001
lt p=0.659
non sib
M. penn.
sib
lt p=0.001
♂♀ lt p=0.001
lt p=0.045
lt p=0.189
q p=0.001
WK 2 4 6

of both species there was a marked decrease in sitting in contact in the fourth week of age, followed by a further increase in this measure.

Mode II interactions and defensive behaviour were omitted from the trend analysis because of their erratic occurrence; instead the data on these behaviours is presented in Tables 3.1 and 3.2 respectively. Since an appropriate statistical analysis was not found for these data, only some observations on the gross appearance of the data are presented here, and later in the text. It is evident from Table 3.1 that the mean frequency of Mode II interactions was highest during the fourth week of age; this was true of all species/sibling/sex classes with the exception of meadow vole ♂♀ sibling and non-sibling dyads, which peaked during the fifth and third week respectively. For both species this peak around the fourth week of age in Mode II interactions coincided with the decrease in scores for sitting in contact by sibling dyads in the fourth week of age. Defensive behaviour was not observed at all between siblings; between non-siblings it did not occur until the sixth week of age.

Differences between the sex classes

The significance of differences between the sex classes at each week of age in scores for nosing of the four different body regions, allogrooming, and sitting in contact were assessed using the *t* test. For meadow voles, no differences between the sex classes were found. For prairie voles, non-sibling ♂♂ dyads in the sixth and seventh weeks of age had lower neck nosing scores than either ♂♀ dyads (2-tailed $P = 0.020$, 6th week; $P < 0.001$, seventh week) or ♀♀ dyads ($P = 0.036$, sixth week; $P = 0.004$, seventh week).

Table 3.1. The mean frequency of Mode II interactions per encounter in each species/sibling/sex/age class.

M. ochrogaster

	sibling				non-sibling			
week	♂♂	♂♀	♀♀	Total	♂♂	♂♀	♀♀	Total
2	0.0	0.3	0.1	0.4	-	-	-	-
3	0.2	0.4	0.4	1.0	0.2	1.5	1.4	3.1
4	1.9	1.5	0.8	4.2	1.3	1.2	1.8	4.3
5	0.2	0.4	0.1	0.7	0.6	0.9	0.2	1.7
6	1.3	0.5	0.3	2.1	0.2	0.0	0.3	0.5
7	0.4	0.8	0.0	1.2	0.0	0.0	0.3	0.3
Total	4.0	3.9	1.7	9.6	2.3	3.6	4.0	9.9

M. pennsylvanicus

	sibling				non-sibling			
week	♂♂	♂♀	♀♀	Total	♂♂	♂♀	♀♀	Total
2	0.3	0.5	0.3	1.1	-	-	-	-
3	0.7	0.1	0.1	0.9	0.1	0.1	0.0	0.2
4	1.7	0.8	0.4	2.9	1.1	0.0	0.0	1.1
5	1.4	0.4	0.0	1.8	0.0	0.5	0.0	0.5
6	0.2	0.1	0.0	0.3	0.0	0.0	0.0	0.0
7	0.1	0.1	0.1	0.3	0.0	0.0	0.0	0.0
	4.4	2.0	0.9	7.3	1.2	0.6	0.0	1.8

Table 3.2 The mean frequency of defensive acts among the different species/sex classes for non-siblings in the sixth and seventh weeks of age.

		♂♂	♂♀	♀♀
M. ochrogaster				
	week 6	2.7	1.0	1.0
	week 7	3.2	1.7	1.7
	total	5.9	2.7	2.7
M. pennsylvanicus				
	week 6	0.0	1.2	0.0
	week 7	0.2	0.4	1.6
	total	0.2	1.6	1.6

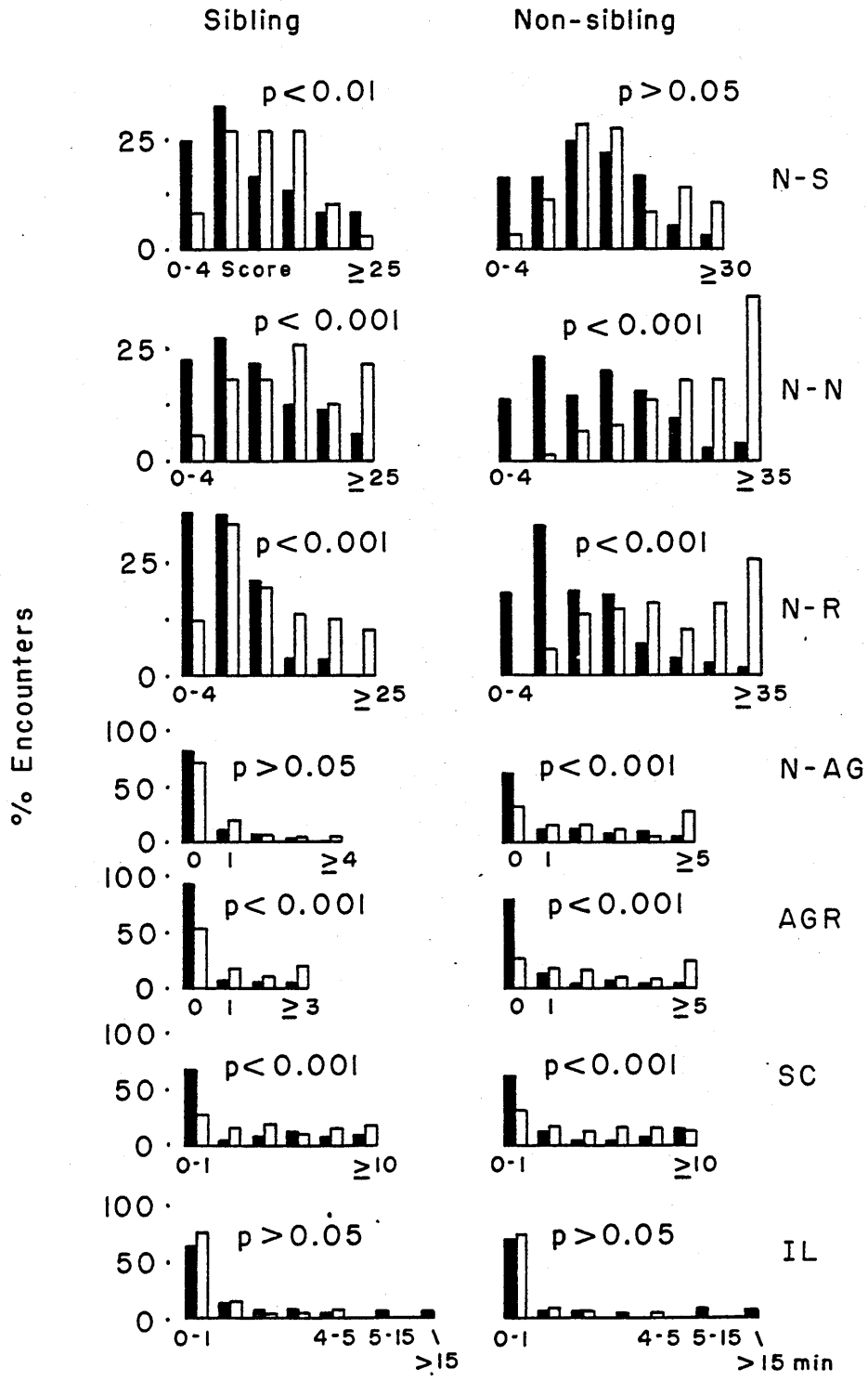
Mode II interactions and defensive behaviour were again considered separately from the above behaviours (see Tables 3.1 and 3.2 respectively) on account of their erratic occurrence. No clear differences between the sex classes in the mean frequency of Mode II interactions were evident in prairie voles, but in meadow voles the mean frequency was relatively high in ♂♂ dyads and low in ♀♀ dyads (Table 3.1). Defensive acts by non-sibling dyads from the sixth week of age were generally most frequent in ♂♂ dyads when prairie voles were considered, but in meadow voles ♂♂ dyads had the lowest mean scores for defensive acts (Table 3.2).

Differences between the species

High and low behaviour scores were found in both species (Fig. 3.4). It was therefore decided that a meaningful approach towards describing species differences would be to consider whereabouts within the range of behaviour scores the largest number of dyads would fall. Accordingly the median test was used (Siegel, 1956). The median test was applied to all encounters in each species/sibling class between the third and fifth weeks of age (Fig. 3.4). Choice of the age range avoids some ontogenetic changes already discussed in the behaviour scores of prairie voles after the fifth week of age, and also avoids the immature behaviour of infants in the second week of age (see below).

Prairie voles had higher median scores for nose-to-neck and nose-to-rump contacts, allogrooming and sitting in contact, whether siblings or non-siblings of the two species were being compared. Prairie voles had a higher median score for nose-to-snout contacts when siblings were compared, but not when non-siblings were compared.

Figure 3.4. Species differences in encounter behaviour scores of sibling and non-sibling dyads between the third and fifth weeks of age. Shaded: M. pennsylvanicus; unshaded: M. ochrogaster. P values indicate the significance level of the species difference assessed by the median test. Abscissa gives behaviour score ranges; ordinate gives the percent of encounters with scores in each range. n, the no. encounters for M. pennsylvanicus are non-sib = 88; sib = 91; and for M. ochrogaster are: non-sib = 90; sib = 90.
N-S: nose-to-snout contact (body nosing scores);
N-N: nose-to-neck contact (body nosing scores);
N-R: nose-to-rump contact (body nosing scores);
N-AG: nose-to-anogenital contact (body nosing scores);
AGR: allogroom (behaviour act scores);
SC: sitting in contact (min);
IL: interaction latency (min).


Sibling
Non-sibling
% Encounters
p<0.01
p>0.05
N-S
25
0
0-4 Score
≥25
0-4
≥30
p<0.001
p<0.001
N-N
0-4
≥25
0-4
≥35
p<0.001
p<0.001
N-R
0-4
≥25
0-4
≥35
100
50
0
p>0.05
p<0.001
N-AG
0 1
≥4
0 1
≥5
p<0.001
p<0.001
AGR
0 1
≥3
0 1
≥5
p<0.001
p<0.001
SC
0-1
≥10
0-1
≥10
p>0.05
p>0.05
IL
0-1
4-5
5-15
>15
0-1
4-5
5-15
>15 min

Prairie voles had a higher median score for nose-to-anogenital contact when non-siblings were considered, but siblings of both species displayed equally low scores for anogenital nosing. There was no difference in the median latencies to interact, even though meadow vole latencies of over five minutes (see procedure for recording encounters) are included in the analysis.

In order to determine the earliest age at which the prairie vole behaviour scores were distinguishably higher than the meadow vole scores, scores for sibling dyads of the two species were compared in the second week of age and again in the third week. The *t* test was used for the comparison, but where the F ratio departed significantly from unity, the non-parametric Kruskal-Wallis analysis of variance was employed to confirm an apparent species difference (Table 3.3). No species differences in body nosing scores were found in the second week of age, although prairie voles spent more time than meadow voles sitting in contact. However, in the third week of age rump and neck nosing scores, as well as scores for time sitting in contact, were greater in prairie voles than in meadow voles.

A Kruskal-Wallis analysis of variance was carried out to confirm that the total nosing scores of wild-caught meadow vole young did not differ significantly from that of lab-reared young tested between weeks three and five. For 15 non-sibling encounters (using a total of 22 wild-caught young) compared to the same number of encounters between lab-reared young selected randomly from comparable age/sibling/sex classes, there was no difference

Table 3.3 Species differences in behaviour scores of sibling dyads in the second and third weeks of age.

Behaviour	mean scores per encounter							
	second week (11-14 days)				third week			
	M. och	M. penn	t test	(F rat. P)	M. och	M. penn	t test	(F rat. P)
snout nosing	10.3	11.8	NS	(1.05 0.90)	12.4	11.2	NS	(3.21 0.002)
neck nosing	16.6	14.2	NS	(1.44 0.33)	17.5	11.1	P=0.02	(1.70 0.15)
rump nosing	11.4	10.4	NS	(2.35 0.03)	13.4	6.7	P=0.002	(4.5 0.00)
sit in contact	8.6	5.5	P=0.01 (P<0.05; Kruskal-Wallis)	(2.2 0.04)	6.1	3.6	(P<0.01; Kruskal-Wallis) P=0.04	(1.1 0.82)
allogroom	0.5	0.03	NS	(94.62 0.00)	1.4	0.13	P=0.009 (P<0.001; Kruskal-Wallis)	(34.59 0.00)

P value of F ratio gives significance of departure of F ratio from unity. Where the t test indicated a significant species difference, but the F ratio departed significantly from unity, the P value of the species difference assessed by the Kruskal-Wallis analysis of variance in also given. NS = non significant difference by the t test.

($\underline{H}$ = 0.167, $\underline{P}$ = 0.5-0.7). The comparison was not carried out for sibling encounters, since in the 3-5 week age range, only four out of 91 meadow vole sibling encounters involved wild-caught young. For these four encounters, snout nosing scores ranged from 9 to 28, and neck nosing scores from 7 to 35, i.e. within the range of scores from the sibling encounters of lab-reared individuals (see Figs. 3.4 and 3.5).

Prairie vole dyads displayed more reciprocity than meadow voles in the number of nosing contacts each vole made to the other as evidenced by correlations between the nosing contact scores made by each member of the dyad (Table 3.4). Further, Mode II interactions were found to consist of more nosing contacts following the initial Mode II act in each interaction in prairie voles than in meadow voles (median number of nosing contacts for prairie voles = 3, for meadow voles = 1; X^2= 23.3, df = 1, $\underline{P}$< 0.001; median test).

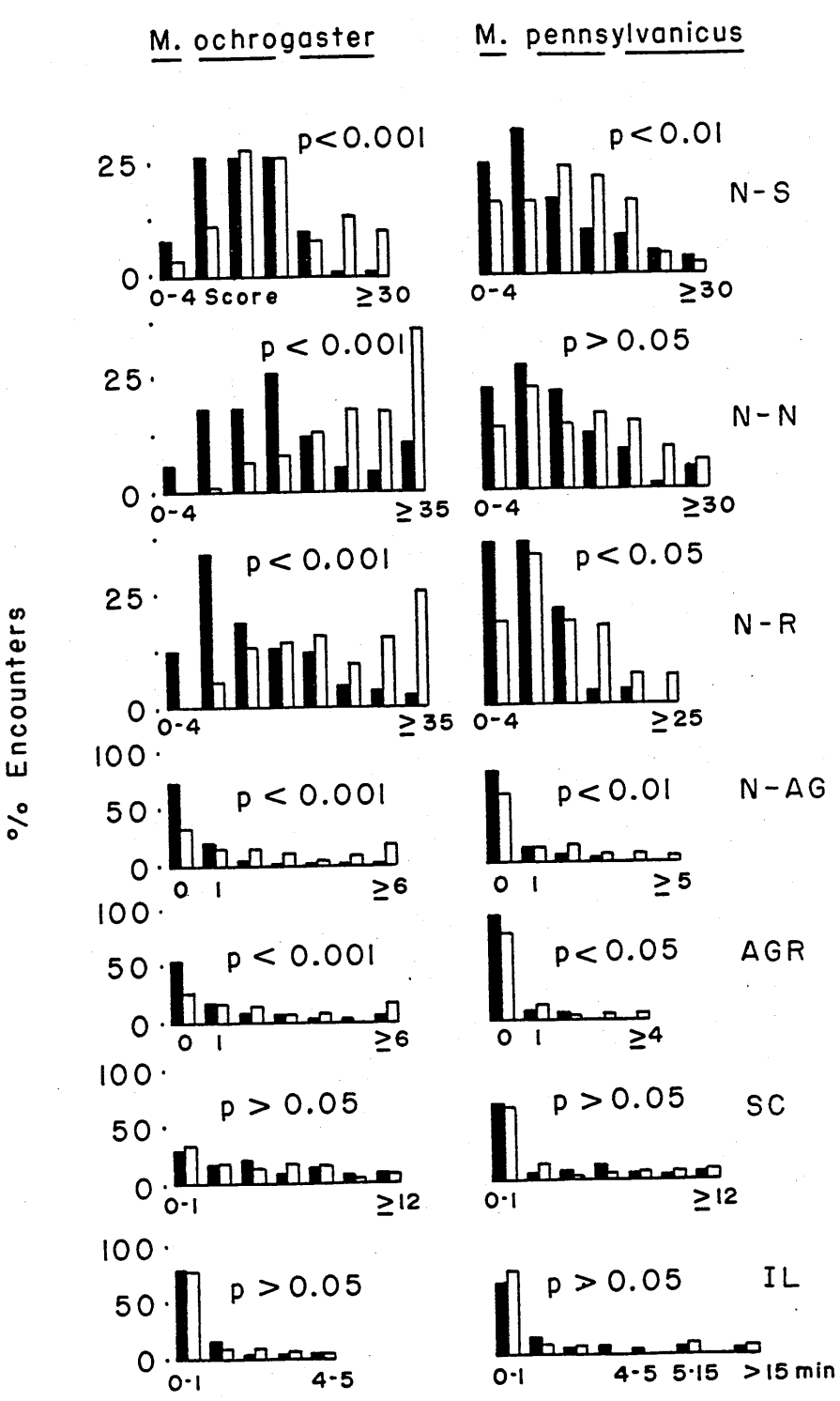
Differences between sibling and non-sibling dyads

The behaviour of sibling and non-sibling dyads was compared by realigning (in Fig. 3.5) the data of Fig. 3.4 in order to contrast the sibling and non-sibling scores for each species; the median test was again used to assess the significance of differences between them. Prairie vole non-sibling dyads exceeded sibling in the median scores for nosing contacts to each body region and for allogrooming at the 1% level of significance. Meadow vole non-sibling dyads also exceeded siblings in the median scores for allogrooming and for nosing the snout, rump and anogenital regions, but the magnitude of the differences

Table 3.4 Correlation between the nosing contact scores by each member of the dyad (weeks 2-7).

		correlation coefficient		
		♂♂	♂♀	♀♀
M. ochrogaster	sibling	0.426 P=0.001	0.452 P<0.001	0.295 P=0.022
	non-sibling	0.424 P=0.002	0.109 P=0.50	0.291 P=0.040
M. pennsylvanicus	sibling	0.153 P=0.244	0.166 P=0.206	0.097 P=0.460
	non-sibling	0.082 P=0.567	0.241 P=0.08	0.078 P=0.619

Figure 3.5. Differences between sibling and non-sibling dyads in encounter behaviour scores of *M. ochrogaster* and *M. pennsylvanicus* between the third and fifth weeks of age. Shaded: sibling; unshaded: non-sibling. *P* values indicate the significance level of the difference between the sibling types assessed by the median test. Abscissa, ordinate, *n*, the no. encounters, and abbreviations are as for Fig. 3.4.


M. ochrogaster
M. pennsylvanicus
% Encounters
p<0.001
p<0.01
N-S
p<0.001
p>0.05
N-N
p<0.001
p<0.05
N-R
p<0.001
p<0.01
N-AG
p<0.001
p<0.05
AGR
p>0.05
p>0.05
SC
p>0.05
p>0.05
IL
25
0
100
50
0-4 Score
≥30
≥35
≥25
0 1
≥6
≥5
≥4
0-1
≥12
4-5
4-5 5-15 >15 min

was less than for prairie voles. Further, there was no difference between meadow vole sibling and non-sibling dyads in the median scores for neck nosing. There was no difference in either species between the sibling types in the median scores for sitting in contact and interaction latency.

Mode II interactions by prairie voles occurred with similar mean frequency in sibling and non-sibling encounters, but Mode II interactions by meadow voles occurred with lower mean frequency in non-sibling than in sibling encounters (Table 3.1). Defensive behaviour was virtually absent from sibling encounters of both species, but occurred during some non-sibling encounters of both species during the sixth and seventh weeks of age (Table 3.2).

DISCUSSION

The results of this study have shown that juvenile prairie voles engaged in more body nosing contacts and huddling than meadow voles, and also differentiated more clearly than meadow voles between siblings and non-siblings in their social behaviour. However, the voles participating in this study undoubtedly do not represent cross-sections of naturally occurring prairie and meadow vole populations accross their range, and caution must be exercised in generalising the results to the species as a whole. The same point was made by King (1958) in reference to his comparative study of behaviour in captive populations of two Peromyscus subspecies. Even in nature, social organisation - and hence the relative frequencies of

different behaviour patterns - may in any case differ in two populations of the same mammal species (Thomas and Birney, 1979; Vestal and Hellack, 1978).

The main result of this study, which may transcend the problems of the origin of the study animals and have general application, is the finding that captive voles from two sources should differ significantly in their scores for body nosing contacts and sitting in contact. Scoring these aspects of behaviour in juveniles might become a useful tool for ranking different populations of small mammals with respect to social tolerance. The results of this study suggest that neck and rump nosing, allogrooming, sitting in contact and Mode II interactions may be the most useful behaviours to score in this respect (snout nosing only exhibited species differences with siblings, and anogenital nosing with non-siblings). The differences in behaviour scores between siblings and non-siblings found in this study suggest a potential for further refinement in classifying species with respect to social tolerance, since the degree of difference between sibling and non-sibling interaction is a reflection of the potential degree of durability and social insulation of sibling relations in nature (Bekoff, 1981). According to the present study, the best indicator of the species difference in sibling/non-sibling disparity in behaviour scores may be neck nosing, since non-siblings displayed significantly more neck nosing than siblings in prairie voles, but not in meadow voles. However, a less dramatic species difference in sibling/non-sibling disparity was also evident in other forms of body nosing. It may be noted

that scores for sitting in contact did not parallel the other social behaviour differences between siblings and non-siblings.

The body nosing behaviour of juveniles has been a much neglected aspect of small mammal behaviour. One reason for this neglect may be that the behaviour lacks an obvious biological goal, and therefore cannot, in our present state of knowledge, be assigned to a functional category such as sexual, parental or aggressive behaviour. The most obvious immediate function of body nosing by prairie and meadow vole juveniles was social investigation, probably resulting in the recognition of an individual as sibling or non-sibling. There is evidence in spiny mice (Acomys cahirinus) that olfactory exchange is necessary for sibling recognition among weanlings (Porter et al., 1978). Possibly the individuals' sex may also be identified, although the results suggest that even if this occurred, it did not significantly influence the interactions of dyads younger than five weeks of age. The frequent repetition of body nosing throughout the encounters suggested that something more than mere recognition or greeting might be taking place. Possibly intensive body nosing may promote the formation of social bonds between the participants. Indeed Happold (1976a) considered that the function of 'attracting' behaviours including body nosing by adult dyads of some conilurine (muroid) rodents was to promote social bonding defined in terms of simultaneous resting in the same nest, nest building, feeding and burrowing by the dyad.

The species/sibling class of juvenile vole dyad with the highest average or median scores for body nosing was the prairie

vole non-sibling class, excepting ♂♂ dyads over five weeks of age. Possible benefit to individual fitness of this intensive body nosing may concern physiological development. Batzli et al. (1977) noted that intimate contact with a non-sibling and unfamiliar conspecific of the opposite sex was necessary for stimulation of sexual development in young prairie voles whose sexual development had been hitherto suppressed owing to the continuous proximity of sibling cagemates. Possibly the highly repetitive nosing contacts to the snout, neck, rump and anogenital regions observed in the non-sibling prairie vole encounters of this study constitute the contact with a stranger necessary for the induction of sexual development. In particular, the high scores for anogenital nosing by non-siblings compared to siblings, and the considerable increase with age in the non-sibling scores, may be important in this respect. Carter et al. (1980) have suggested that reproductive activation of young female prairie voles may be stimulated by direct naso-genital contact, and they have observed that siblings in their home cages rarely make this contact. My results are in agreement with their suggestion. Possibly nosing contacts to the other body regions may also contribute to physiological development - or may function to establish the social tolerance necessary for repeated anogenital nosing to be permitted. The considerable degree of reciprocity observed in prairie vole nosing contacts may be understood if it is to the advantage of <u>each</u> member of a non-sibling dyad to nose the other as much as possible.[1]

The large amount of body nosing observed between prairie vole non-siblings may also be necessary to generate a social bond

[1]Such a mutual benefit would be difficult to establish experimentally.

between a juvenile and a strange conspecific against the background of strong sibling ties (see Bekoff, 1981). The formation of heterosexual pair-bonding probably increases the chance of reproductive success in prairie voles (Thomas and Birney, 1979); intensive body nosing between a juvenile and a stranger might in any case encourage dispersal of prairie vole young away from their parents' extended family. The relatively less intensive body nosing observed in meadow vole non-sibling encounters is consistent with the fact that meadow vole young apparently do not show sibling suppression of sexual development (Batzli et al., 1977), and therefore have no need for sexual development to be induced by interaction with a stranger Further, there is probably no strong background of sibling cohesion to be overcome by the attraction of a stranger in order for dispersal and reproduction of young animals to proceed.

A bell-shaped curve during ontogeny and sex differences were found for the distribution of Mode II interactions in both species, while overall nosing scores did not correspond with these findings. These results suggest that Mode II behaviour may play a role in vole development which is quite distinct from that suggested for overall body nosing, which is largely mode I behaviour. Bekoff (1976) suggested that there should be a bell-shaped curve for the ontogeny of the amount of social play by young mammals, with the age corresponding to the peak of the curve as the 'socialization period'. If Mode II interactions are considered to be a form of play (see section on social behaviour recorded), Bekoff's hypothesis might suggest that the post-weaning period centering on the fourth week of age - when

the maximum number of Mode II interactions were seen - may be an important period for socialisation of juvenile voles amongst their agemates. The decrease in sitting in contact by siblings at this age may reflect a higher activity level during this socialisation period.

To conclude, this study found that social behaviour displayed by juvenile dyads of two Microtus species consisted of repeated contacts of a gentle and unhurried nature as well as continuous contact; the behaviour lacked an obvious biological goal. Nevertheless, quantitative differences in the behaviour were found between the two species and between sibling and non-sibling dyads; these differences may lie at the root of the species differences in social organisation. This study has therefore focussed attention on a much neglected aspect of small mammal social behaviour, i.e. that of juveniles. It is to be hoped that this and future studies of juvenile social behaviour may complement recent and current studies of sexual behaviour (e.g. Gray and Dewsbury, 1973), aggressive behaviour (e.g. Getz, 1962; Krebs, 1970; Rose and Gaines, 1976; Rose, 1979), mating systems (e.g. Thomas and Birney, 1979; Stehn and Richmond, 1975; Batzli et al., 1977), parental behaviour (e.g. Hartung and Dewsbury, 1979; King, 1958; see also Chapter 2) and spatial organisation in the field (e.g. Madison, 1980) in furthering our understanding of species differences in small mammal social organisation.

CHAPTER 4

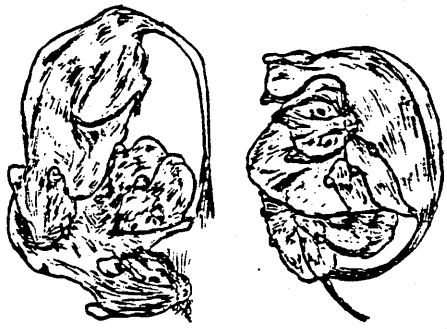
CONTACT-PROMOTING BEHAVIOUR, SOCIAL DEVELOPMENT AND RELATIONSHIP WITH PARENTS IN SIBLING JUVENILE DEGUS (*OCTODON DEGUS*)

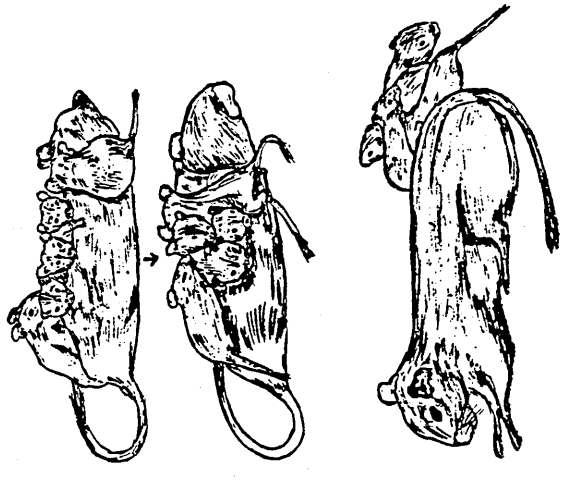
FRONTESPIECE

Bodily contact between parents and young
in *Octodon degus*

left- mother and young; centre- father and young; right- father (on top), mother and young.

Sketches are drawn from observation





ABSTRACT

This chapter describes infant socialisation in captive parent-young units of the caviomorph rodent Octodon degus. Types of parent-young contact (huddling or squatting) and social interaction (body nosing and accompanying behaviours) are described and their ontogenetic trends examined between post-natal days one and 46. Fathers spent less time than mothers in contact with the young. Mother-young contact decreased post-natally, whereas the amounts of mother-young and father-young social interaction, measured in terms of body nosing exchanges, showed a continuous increase post-natally; sibling interactions also showed a continuous increase. Father-young interactions tended to be dominated by the father. Young reared with the father cohabiting huddled less with their mother, and engaged in less body nosing, than young reared in the father's absence. Observations suggested that paternal control of the young may curb juvenile interactions. Young observed without their parents in an unfamiliar enclosure did not groom or 'play' as in their home cage with their parents present, but engaged in relatively more vocalising, neck nosing and forepaw-clasping.

INTRODUCTION

The degu (Octodon degus) is a rat-sized caviomorph rodent found in the low-lying grasslands of central Chile (Woods and Boraker, 1975). Degus live communally, in non-overlapping groups, each of which includes several adults of both sexes (Fulk, 1976). They are diurnal, active animals which engage in considerable huddling, social grooming and social play as juveniles, and vigorous interaction as adults (Wilson and Kleiman, 1974; Kleiman, 1974; Davis, 1975; Fulk, 1976; Yanez and Jaksic, 1976). They make extensive use of urine marking (Kleiman, 1975) and of their vocal repertoire (Eisenberg, 1974; Reynolds and Wright, 1979). The young are considered to be semi-precocial, being fully furred and with open eyes at birth, and able to walk in a wobbly fashion. The aims of this chapter are to examine contact-promoting patterns used by sibling infants and juveniles in captivity, and to trace the progress of social relationships among littermates and between young and their parents in captivity by quantifying the occurrence of different types of social interaction during juvenile ontogeny.

In an earlier study of this species in captivity (Wilson and Kleiman, 1974), body nosing contacts between animals were identified as a dominant mode of juvenile social interaction, although distinguishable vocalisations (see also Reynolds and Wright, 1979) and body postures may often accompany body nosing.

A striking aspect of this earlier study was the similarity in juvenile social behaviour patterns between Octodon and a vole species also studied earlier (Microtus agrestis; Wilson, 1973). Behavioural similarities in Microtus and Octodon included the frequent use by juveniles of brief body nosing contacts to one another, the body areas nosed, and head-shaking, jumping and running which often accompanied body nosing, and appeared to be an immediate consequence of it. In Chapter 3 of this thesis, body nosing contacts were shown to be the principal observable mode of juvenile social interaction in the voles Microtus ochrogaster and M. pennsylvanicus. The present study of Octodon is a continuation of this series of studies of juvenile body nosing behaviours, and body nosing contacts are used as the principal indicator of the amount of ongoing social interaction among juveniles and between juveniles and their parents.

Thus the emphasis on behaviour recorded in this chapter is the same as that in Chapters 2 and 3, and the methods of recording and classifying behaviours are also the same. Whereas the vole study was separated into a consideration of parent-young contact (Chapter 2) and juvenile social interactions (Chapter 3) because these aspects of behaviour were most readily observed in different contexts, parent-young contact and juvenile social interactions in Octodon were both readily observed in the single context of undisturbed family groups; observations of both of these aspects of behaviour are therefore presented here together in one chapter.

ANIMALS AND METHODS

Animals and enclosures

The Octodon degus colony at the National Zoological Park was derived from four adults received in 1971 from a colony initiated in 1964 at the Massachussetts Institute of Technology.

Living enclosures for family groups, in which observations of the families were made, consisted of glass-fronted wooden cages each measuring about 100 x 60 x 50 cm. The substrate was pine shavings. Each cage contained a nest box with sides of transparent plastic, a large wooden block for gnawing and climbing on, and a metal tray containing sand. Nesting material in the form of shredded newspaper was given only at the time of birth, since the animals did not use it at other times. Dry food (seeds, nuts, grains and rabbit chow) were fed daily, and supplemented daily with fresh kale along with other fresh vegetables and fruit. Water was always available.

Observations

Three series of observations were carried out:
(1) Family units consisting of a litter and either the mother or both parents were observed from the day of birth (day one) through day 46; this is the age at which degu young approach puberty (Wilson, unpublished observations[1]).

In the first condition the father was housed continuously

[1]After this age vaginal opening began to occur, and social interaction between non-siblings during dyadic encounters incorporated many components of aggressive behaviour not occurring earlier in ontogeny.

with the mother from mating through the birth of the litter and until observations ceased. Five such families were observed, involving five different mothers and four different fathers. The mean litter size was 6.4 (range 5-8) and the mean sex ratio was 4.2♂♂:2.0♀♀. In the second condition the mate was removed before the birth. Five such mother-litter groups were observed, involving five different females (four of these females were also observed in the father-present condition, two of them before they reared their young alone, and two after rearing their young alone). The mean litter size was 4.8 (range 3-7), and the mean sex ratio was 1 ♂:1.18♀♀. Differences between the two conditions in mean litter size and sex ratio were considered during data analysis.

The first five family units (two with the father absent) were housed at the National Zoological Park, on a light cycle of 12 hours light and 12 hours dark, darkness beginning at 15:30. The remaining five family units observed were housed in the basement of the author's home, where the light schedule was natural dim daylight supplemented by dim electric light in the evening. The room was usually in darkness for five to eight hours at night. Temperatures at both locales were maintained between about 65 and 75 F according to season.

Each family was observed six or seven days a week for two daily 15-min periods. The 15-min period is an arbitrarily defined segment of time which has been used for other authors charting the ontogeny of juvenile and parent-young social behaviour in

captive rodents (Kleiman, 1972; Happold, 1976b; it is also the same time period as that used for observing vole parent-young contact in Chapter 2). Animals housed at the zoo were observed once in the late morning, and again in the early afternoon; this schedule avoided feeding and cleaning times, and the onset of darkness. For the animals housed in the author's home, the two 15-min observation periods were chosen on an ad libitum basis, but were always separated by an interval during which the animals were (as at the zoo) given fresh food. The interval was at least $2\frac{1}{2}$ hours (as for the observations of vole families; Chapter 2).

Observations were handwritten, using a behaviour code. Behaviour was recorded in terms of the following measures:

Contact time:- time spent in continuous body contact (either nursing or huddling) between one or both parents and at least one young; the converse measure of parental time off the young was also used.

Body nosing scores:- Most body nosing contacts were brief (i.e. less than two sec) and received a body nosing score of one. The nosing score was adjusted in the case of longer contacts; those lasting two sec or longer received a score of two. Allogrooming, in which an animal nibbled and licked another's fur, was considered to be a form of body nosing and was scored as above; However, prolonged, unbroken bouts of allogrooming received a maximum nosing score of four. This method of scoring body nosing contacts is the same as that used during the vole study (Chapters 2 and 3).

Body nosing scores were attributed to the class of animal doing the nosing (i.e. young to each other, young to their parents, and parents to young), and all scores for each observation were divided by the number of young in the litter.

Behaviour act scores:- The occurrence of selected behaviour patterns was measured by each performance of a behaviour pattern receiving a behaviour score of one, regardless of duration. As for body nosing scores, behaviour act scores were attributed to the class of animal performing the behaviour (i.e. young to each other, young to parents and parents to young), and all scores for each observation were divided by the number of young in the litter. The behaviour patterns selected for this measurement have been collectively termed 'play' when performed by juveniles in their home cage, and are described in detail in the earlier study (Wilson and Kleiman, 1974). When young nose one another, they sometimes engage in physical manoeuvres involving loose body tone. These include one animal forepaw-clasping another from the rear position, and young (usually a dyad) adopting a venter-to-venter orientation in the mutual-upright or, occasionally, the supine-quadrupedal position. In the mutual-upright position, the young push against each other's shoulders. These behaviours are almost always accompanied by the 'gurgling' vocalisation (Reynolds and Wright, 1979). Each occurrence of snout or neck nosing not in the context of any of the above manoeuvres or allogrooming also received a behaviour act score of one, classified as 'nosing in unstereotyped positions'. (rump and anogenital nosing, and allogrooming, were also scored in this manner, but the data have not been included here).

Locomotor-rotational movements sometimes accompany juvenile body nosing behaviours, and each occurrence received a score of one under 'jumping' or 'headshaking' respectively. This behaviour act scoring method is comparable to that used for the behaviour of juvenile voles in the vole dyadic encounter study (Chapter 3).

(2) For the second series of observations. litters were removed from their home enclosure and parents, and placed in a separate enclosure; the substrate was pine shavings with a sand patch. Each litter was observed in this enclosure for 10 min on post-natal days 2,4,6,8,10,12,14,17,19 and 21; the observation was kept to 10 min in order to minimise stress and heat loss to young infants. Five such litters were observed (mean litter size 5.6, range 3-8) during the illuminated hours at the author's home; these observations were not carried out on each day until after the daily observations of family units in their home cages were completed. The general behaviour of young in the separate enclosure without their parents was recorded; the number of nosing contacts made to the snout, neck and rump were counted, and divided by the number of young in the litter for each observation.

(3) Sibling dyads (♂♂, ♂♀ and ♀♀) were removed from their home enclosure and parents, and placed in a separate enclosure; the substrate was pine shavings with a sand patch. Each dyad was observed for 15 min. Individuals were observed not more than once in each sex combination at ages corresponding to weekly intervals from the second to the seventh week of age (this method is

comparable to that used for vole dyadic encounters described in Chapter 3). Data from 36 such encounters are summarised here. Ten individual females and 12 males from six litters are represented in these data; some animals were reared and tested at the zoo; others at the author's home. The general behaviour of the dyad was recorded; the number of nosing contacts made to the snout, neck, rump and anogenital region were counted, and it was noted whether or not a nosing contact was accompanied by forepaw-clasping. The number of times forepaw clasping occurred was also counted. Encounters between non-sibling dyads were also carried out, as in the vole study (Chapter 3), but insufficient data was obtained, owing to the infrequent occurrence of simultaneous births in our Octodon colony, and hence insufficient availability of non-siblings of the same age (see Chapter 1).

RESULTS

(1) Observations of undisturbed family units.

Data distribution Because of the ad libitum method of sampling undisturbed behaviour of family groups, the scores for active behaviours and parent-young contact time varied according to the phase of the activity rhythm sampled. The data are therefore highly skewed, rendering standard measures and analyses of variance inappropriate. The purpose of this type of data collection was to obtain sufficiently large samples of degu behaviour, covering a number of different individuals at all phases of the activity cycle, to arrive at estimates of the average amount of each activity and parent-young contact occurring per unit time at any given age of the young (see also Chapter 2; the same type of data collection was used in observations of undisturbed vole family groups).

Data for body nosing scores and parent-young contact time have been considered in successive three-day periods (the final period, d 43-46, is actually a four-day period). Since in each condition (father absent or present) five families were generally observed twice daily, the maximum number of observations in each three-day period was 30, each family being represented by six observations (in practice, the three-day period sample size is sometimes less than 30 (Fig. 4.1), since the first five litters were only observed six days a week).

For each three-day period the mean scores for body nosing and parent-young contact rather than the medians are presented.

Since the method of data collection used in this study was an effort to sample all phases of the activity cycle, it was important for a representative portrayal of the overall amount of social activity at different ages that zero body nosing and behaviour act scores (when the animals are resting) be incorporated, and also that the exact magnitude both of low body nosing and behaviour act scores of infants engaging in their first social interactions and the high scores of older young be taken into account. The mean score is used here since it takes greater account of scores at the high and low end of the range than does the median (Ferguson, 1966).

Regressions have been calculated in order to assess the significance of apparently linear ontogenetic trends in the mean scores for successive three-day periods.

Since the three-day means for behaviour act scores for each behaviour pattern, such as forepaw-clasping or interaction in the venter-to-venter position, fluctuated more than body nosing scores on account of the relatively erratic occurrence of individual patterns, behaviour act scores are presented there as six-day means in order to present any ontogenetic trends more clearly.

Parent-young contact The mean time spent by mothers in continuous contact with the young (Fig. 4.1) decreased linearly from birth in both the father-present and father-asent conditions (b, the slope of the calculated regression line, = -0.13; r = -0.90, $P < 0.01$ for father-present; b = -0.13; r = -0.85, $P < 0.01$ for father-absent). However, the data in Fig. 4.1 suggest that this linear decrease may not continue beyond about six weeks of age; this is in fact the age at which nutritional weaning is thought to be

complete (Kleiman, 1974; Reynolds and Wright, 1979).

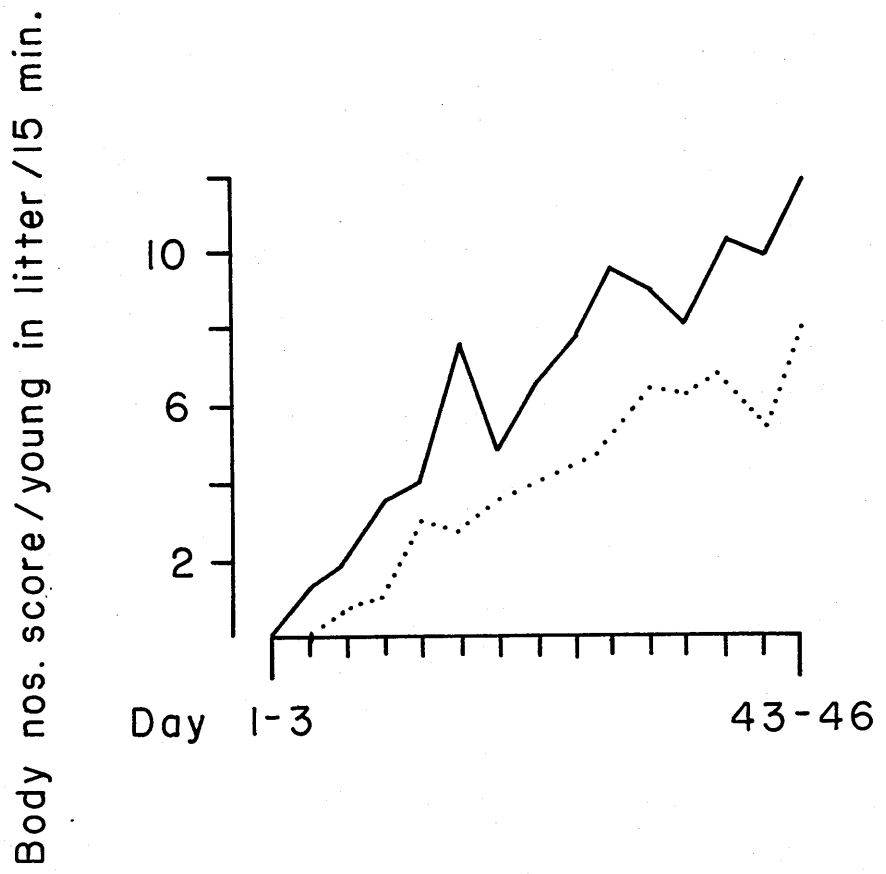
Degu fathers enthusiastically sought access to the young (see also Kleiman, 1974). They squatted over, licked and groomed small young, and huddled over them as they grew older. The young pushed under the father in the supine position as often as they did under the mother (129 and 128 times respectively for all observations of litters reared by both parents). The data in Fig. 4.1 indicate that fathers spent considerable time with the young, although much less than did the mothers. When the father lay together with the mother and young, the family usually huddled with the father near the top. The father rested with the mother and young on average 4.5 min per 15 for the first 30 post-natal days, and only 2.7 min thereafter (Fig. 4.1, 2-tailed $P < 0.002$ by the Mann-Whitney U test, comparing daily means for days 1-30 with days 31-46).

The ontogeny of juvenile social interaction The first day on which young were seen to leave the nest box during observation periods ranged from the third to the fifth post-natal day ($\bar{X}$ = 3.3d). However, social interaction between siblings was occasionally observed before this age in the nest while the mother or both parents were absent. When alone, newborn young would jostle for individual position, with young on the periphery of the group pushing towards the top and centre. As an infant crawled over its siblings, its nose sometimes brushed against the neck of a littermate beneath it. Very occasionally a nose-to-snout contact occurred. Up to ten days of age, an infant pushing over the heap of littermates would occasionally sniff the neck or snout of a sibling, give a head-shake or jump, and then

Figure 4.1. Time spent by parents in contact with young. _____, mother; ------, father; ....., mother and father in nest together; . . . ., either parent.

n no. 15 min. obs. bouts
x̄ time/15 min. obs. bout
14
12
10
8
6
4
2
Day
1-3
7-9
13-15
19-21
25-27
31-33
37-39
43-46
Father present
Father absent
28 28 30 30 28 30 26 28 28 26 28 26 30 34
30 26 28 28 28 30 26 30 27 28 26 28 21 33

Figure 4.2. Body nosing scores for sibling interactions. _____, father absent; ....., father present.


Body nos. score / young in litter / 15 min.
10
6
2
Day 1-3
43-46

run out of the nest with a sibling sometimes running after it.

Neck nosing, usually the first pattern to appear ($\bar{X}$ day = 3.92, ramge 1-10), was followed in ontogeny by snout nosing ($\bar{X}$ day = 6.00, range 3-14), head-shaking ($\bar{X}$ day = 8.38, range 6-13) and forepaw-clasping ($\bar{X}$ day = 11.0, range 5-15). This ontogenetic order was highly consistent over all litters (Kendall's coefficient of concordance, W, = 0.69, $\underline{P} < 0.001$).

The mean body nosing scores for sibling interactions increased linearly with age from birth through day 46 (Fig. 4.2; $\underline{r}$ was significant at the 1% level for both the father-present and father-absent conditions). When the behaviour patterns were considered separately (Fig. 4.3; neck and snout nosing in unstereotyped positions and venter-to-venter interactions were found to increase linearly with age ($\underline{r}$ was significant at the 5% level in all cases), while head-shaking, jumping and forepaw-clasping did not.

The mean body nosing scores for parent-young interactions also increased linearly with post-natal age (Fig. 4.4; $\underline{r}$ was significant at the 1% level in all cases). The scores for mother nosing the young and for young nosing the mother show similar trends, suggesting that mother-young interactions were largely reciprocal. However, the fathers' mean contribution to nosing scores for father-young interactions consistently exceeded that of the young throughout the developmental period observed (Fig. 4.4). When the data for sibling nosing scores (Fig. 4.2) are compared with young-to-parent nosing scores (Fig. 4.4), it is evident that the young generally nosed each other more than they did either of their parents.

Fig. 4.3. Behaviour act scores for sibling interactions. _____, father absent; ....., father present. (a) snout nosing, (b) neck nosing, (c) venter-to-venter interactions, (d) forepaw-clasping, (e) head-shaking, (f) jumping.

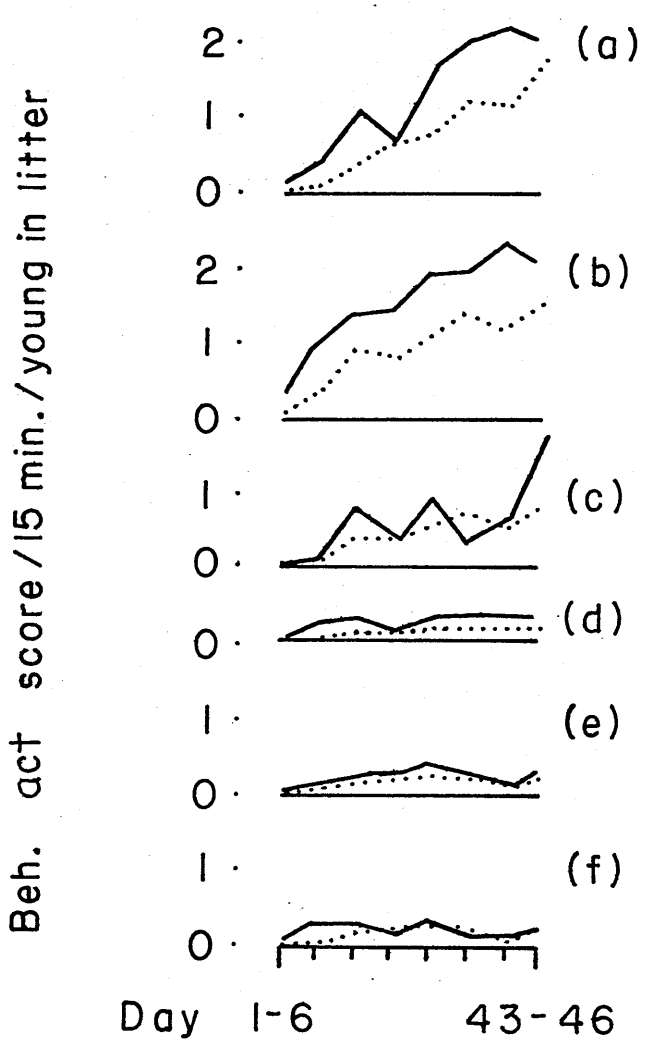
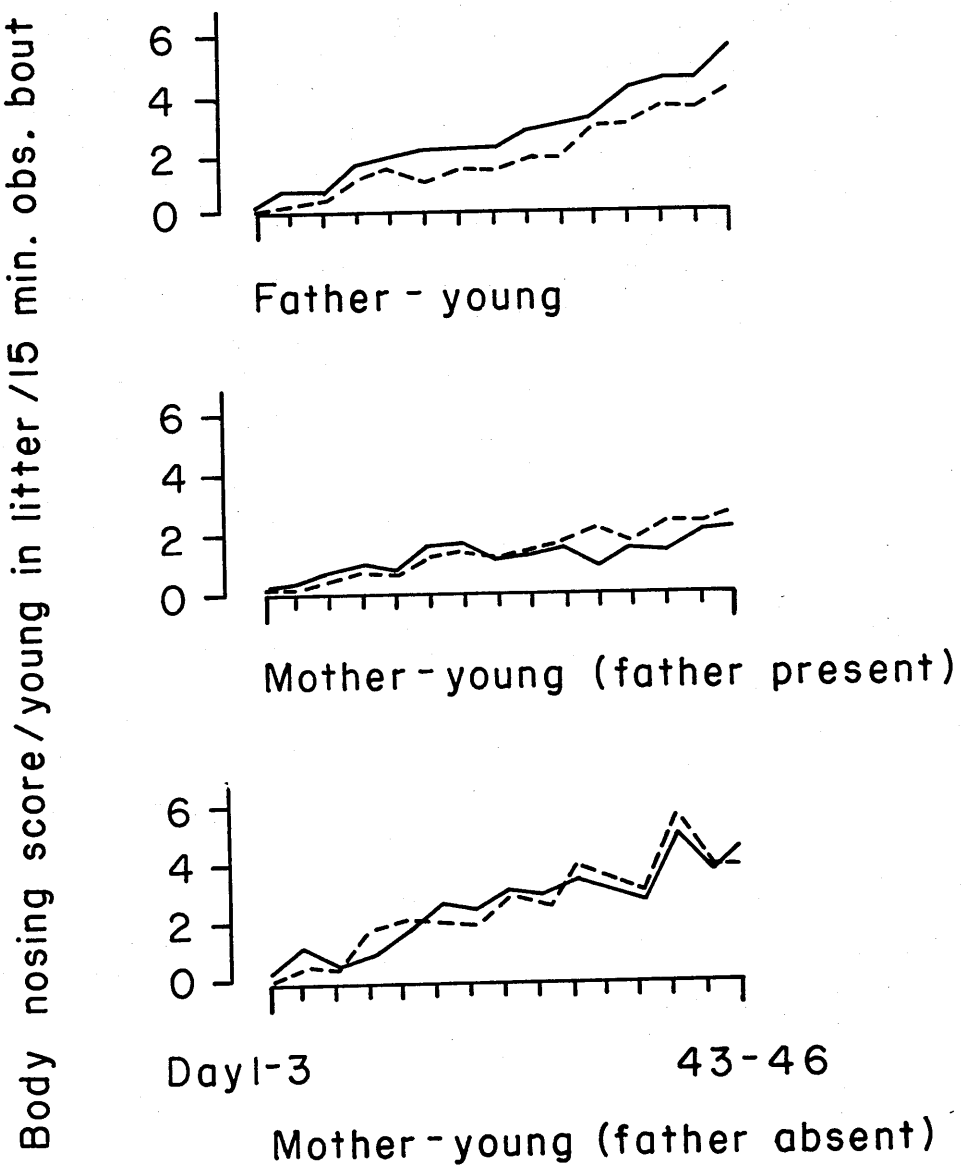

Beh. act score/15 min./young in litter
2
1
0
(a)
(b)
(c)
(d)
(e)
(f)
Day 1-6
43-46

Figure 4.4. Body nosing scores for parent-young interactions. ———, parent; ------, young.


Body nosing score/young in litter/15 min. obs. bout
6
4
2
0
Father - young
6
4
2
0
Mother - young (father present)
6
4
2
0
Day 1-3
43-46
Mother - young (father absent)

The effects of cohabitation by the father on social behaviour of the family unit Cohabitation by the father resulted in the mother spending slightly less time in contact with the young than in his absence (2-tailed $P < 0.002$ by the Wilcoxon matched pairs test, comparing mean contact time for the five litters in each condition for each post-natal day 1-46). Huddling by the young over the mother was observed in the father-absent, but not the father-present condition.

Litters reared in the father's presence engaged in less body nosing amongst themselves (Fig. 4.2) and with their mother (Fig. 4.4) than in the father-absent condition ($P < 0.002$ in both cases by the Sign test, comparing mean nosing scores for the five litters in each condition for each post-natal day 1-46).

Since the average litter size of litters reared in the father's absence was smaller than that of the litters reared in his presence, the possibility of litter size affecting the per-animal nosing scores was investigated. The per-animal nosing scores for littermate interactions were compared between days 36 and 46 in two litters (#8 and #13) with three young in each, and two litters (#7 and #15) with seven and eight young respectively. All four litters were reared in the father's absence. A Kruskal-Wallis analysis of variance indicated no difference ($P = 0.2$-0.3) between the scores for the two sets of litters. The litters raised in the two conditions (father-present and father-absent) also had different mean sex ratios. However, this difference is unlikely to have contributed to the higher scores in the father-absent litters, since there

were proportionately fewer males in this group, and males are thought to be the more socially active sex in Octodon degus (Kleiman, 1974; 1975).

When the different components of sibling interaction were considered, the young reared in the father's presence engaged in fewer snout and neck nosing contacts (2-tailed $P < 0.02$ by the Sign test in both cases) and did less forepaw clasping ($P < 0.05$ by the Sign test) than did the young in the father-absent condition. However, the mean frequencies of interactions in the venter-to-venter position, head-shaking and jumping did not differ in the father's presence and absence (Fig. 4.3).

Young reared in the father's absence received consistently higher mean scores for body nosing of other siblings and the mother than did young reared in the father's presence for body nosing of all family members ($P < 0.002$ by the Sign test for days 1-46, averaging 36% higher between days 22 and 46). The lower body nosing scores for sibling and mother-young interaction in the father-present condition are not therefore a mere consequence of some of the juveniles' attention being diverted from each other and their mother to another adult; they actually did less nosing in total.

The correlation between juvenile body nosing scores and the amount of time young were not in contact with a parent was positive and significant for litters reared in the father's absence (partial correlation coefficient with the effect of age eliminated = 0.56, $P < 0.05$), but not for those reared in his presence ($r = 0.22$, $P > 0.20$). The unpredictable rate of body

nosing among siblings during activity periods in the father-present condition suggests a direct effect of the father on juvenile social interaction. Indeed, all four Octodon fathers sometimes caused the separation of young engaged in vigorous social interaction by squealing at them (38 occasions) and by pushing the young apart (23 occasions). The father occasionally sniffed, groomed or forepaw-clasped the young he separated. Fifty-one of 61 cases of juvenile separation occurred after the fourth week of age. These interruptions apparently inhibited juvenile activity only briefly, the young usually resuming interaction as soon as the father turned away.

Fathers groomed young about twice as often as did the mothers (685 paternal versus 307 maternal instances of grooming in the father-present condition). Young would solicit grooming from the father (and mother) by pushing under his chin and tapping his head with a forepaw, but they reciprocated the grooming only about half of the time (340 instances of grooming of the father by the young). From the end of the third week of age, the father sometimes pursued and forepaw-clasped the young, always while emitting the non-aggressive 'gurgling' vocalisation (Reynolds and Wright, 1979). The young occasionally protested by struggling or squealing, but usually moved forwards with the father still mounted. Forepaw clasping by the father often ended with pelvic thrusting followed by dismounting and penile grooming. There were a total of 167 instances of paternal forepaw-clasping, but only five of forepaw-clasping by the mother in the father-present condition.

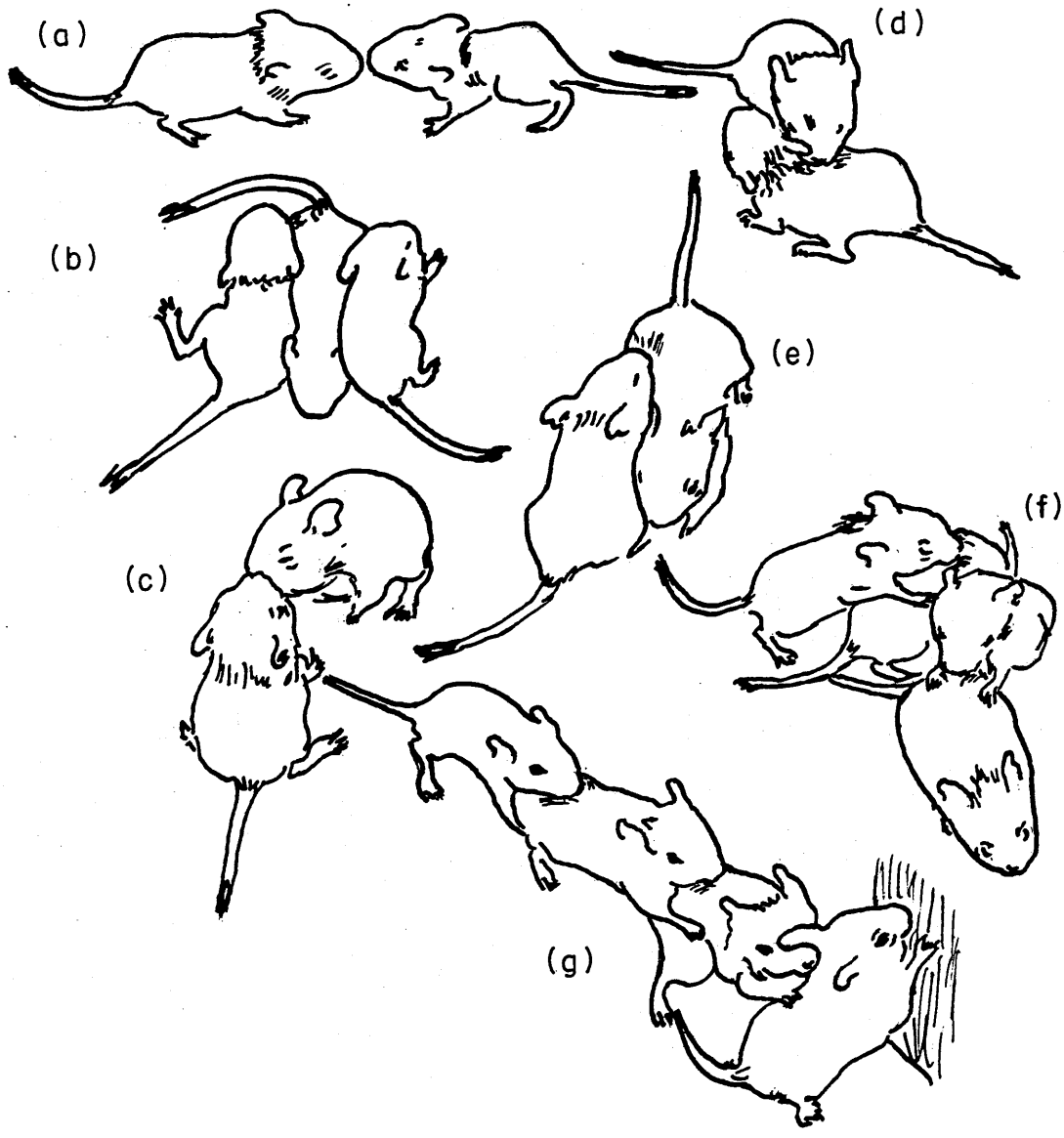
(2) Observations of litters removed from their parents and home enclosure.

When placed in the unfamiliar enclosure, an infant not in contact with a sibling would emit an 'isolation' call, a piercing squeal characteristic of several caviomorph species when infants are separated from their parents (Eisenberg, 1974; Reynolds and Wright, 1979). Squealing young moved around until they encountered one or more littermates (Fig. 4.5a). Upon meeting they would emit the 'gurgle' or louder 'whistle' vocalisation (Eisenberg, 1974; Reynolds and Wright, 1979) and push into side-to-side contact (Fig. 4.5b).

As the young grew older, they moved actively around the enclosure and interacted with each other before congregating into a huddle. The age at which a litter remained active without emitting the isolation call for the entire 10-min observation period ranged from eight to 17 days, according to the litter.

Interaction initially consisted of brief nosing contacts directed at the snout, neck and rump regions (Fig. 4.5 c,d and e). From the second week of age, urine marking occurred in the depressed-rump posture characteristic of Octodon (Kleiman, 1975); sandbathing also occurred from this age (see Wilson and Kleiman, 1974, and Eisenberg, 1967 for description of sandbathing behaviour). Towards the end of the second week of age, young sometimes made forepaw contact with a companion's back or rump while nosing the neck or rump respectively (Fig. 4.5f). From the third week of age, true forepaw-clasping of the companion's back or rump occurred (Fig. 4.5g), especially towards the end of a 10-min observation

Figure 4.5. Behaviour of infant degus in unfamiliar enclosure. (a) mutual approach (1st week), (b) huddle (1st week), (c) snout nosing (2nd week), (d) neck nosing (2nd week), (e) rump nosing (2nd week), (f) nosing with forepaw contact (2nd week), (g) contagious forepaw-clasping (3rd week). Drawn from photographs.


(a)
(b)
(c)
(d)
(e)
(f)
(g)

period. It was sometimes triggered by one or more infants emitting the isolation call which results in others approaching, and a littermate group circling and nosing one another while squealing. More young sometimes approached the initial forepaw-clasping dyad, and joined on the end, forming a 'train' (Fig. 4.5g).

The number of nosing contacts to the snout, neck and rump regions were counted on each day of observation for all five litters. The mean per-young number of neck nosing contacts ranged from less than two per observation on d2 to 10 on d21, whereas snout and rump nosing contacts ranged from less than one per observation on d2 to a maximum of four; the Mann-Whitney U test on daily counts for each litter of per-young nosing contacts indicated that neck nosing exceeded nosing of the snout and rump during the second and third week of age (2-tailed $P < 0.002$ for both neck vs. snout nosing and neck vs. rump nosing). The Mann-Whitney U test also indicated that the frequencies for nosing all three body regions were greater during the second than the first week of age ($P < 0.002$ in each case); frequencies for neck and snout nosing were also greater in the third week than the second week of age ($P < 0.02$ in each case), but rump nosing did not increase.

(3) Observations of sibling dyads removed from their parents and home enclosure.

The behaviour of sibling dyads aged two to seven weeks was similar to that of whole litter groups; however, no progressive increase with age in body nosing frequencies was detected during

this period. Neck nosing accounted for 54% of all nosing contacts, snout nosing for 17% and rump nosing for 27%. Anogenital nosing, which had not been observed in litter groups up to three weeks of age, accounted for a total of 2%. The number of nosing contacts to the neck exceeded those to the snout in all but two of the 36 encounters, and those to the rump in all but five encounters. Forepaw-clasping accompanied by 'gurgling' was a prominent behaviour of ♂♂ dyads ($\overline{X}$ = 12 per observation, range 1-61) and of ♂♀ dyads ($\overline{X}$ = 12, range 3-23), but occurred less commonly with ♀♀ dyads ($\overline{X}$ = 3, range 0-9). Between a male and a female, the male would do most of the forepaw-clasping. Of nosing contacts <u>not</u> accompanied by forepaw-clasping, ♂♂ and ♂♀ dyads performed almost equally ($\overline{X}$ = 44.0 and 43.3 respectively, range 27-54 in both cases) and more than ♀♀ dyads ($\overline{X}$ = 34.8, range 9-54, 2-tailed $\underline{P} < 0.05$ by the Mann-Whitney U test for both ♂♂-♀♀ and ♂♀-♀♀ comparisons).

DISCUSSION

Contact between mother and young consisted of nursing, squatting and huddling, which decreased with increasing post-natal age, and body nosing which, conversely, increased with post-natal age. Thus between mother and young there appeared to be a gradual changeover during ontogeny of the relationship from one of caregiving/dependence to one of mutual body sniffing, grooming and huddling. Such a post-weaning continuation of the mother-young

relationship is considered to be a possible basis of social organisation in many group-living mammal species (Horwich, Dyke and Cogswell, 1977).

All four individual fathers were highly tolerant and solicitous of their young; they nosed, groomed, squatted over, and later huddled on them. Father-young body nosing increased with post-natal age, with the father nosing the young on average more than the reverse. Social grooming, particularly by the father, was a prominent feature of their interactions. All these behaviours by the father towards the young would be included in the category of direct investment by the male parent, defined by Kleiman and Malcolm (1981) as care of the young which has "....an immediate physical influence on them which increases 'survivorship'." Nevertheless, the ways in which the degu father may benefit his young are not immediately obvious from this study of his paternal behaviour. Mothers actually spent less time in contact with their young in the father's presence than in his absence. The results indicate that the father participated in parent-young contact without effectively increasing it. This conclusion resembles that reached by Tasse (1981) in her study of another caviomorph, the rock cavy (Kerodon rupestris): although the father participated enthusiastically in huddling with the young, the infants actually made poorer weight gain when the father cohabited than they did in his absence.

Thus some kind of paternal physical influence on the young other than promotion of physical development needs to be suggested.

Possibly through the intense father-young contact and interaction, which tended to be dominated by the father, the father may increase his control of the young, and gain sociosexual dominance over them. Paternal forepaw-clasping in degus resembles 'sociosexual mounting' in primates, which is considered to be "...a basic part of a primate male's repertoire that gains him non-aggressive contact with other males and females..", and may include elements of dominance and 'reassurance' (Hanby, 1976). The results indicating lower sibling and mother-young body nosing scores in the father-present condition, considered together with observations of paternal huddling, grooming, forepaw-clasping and interruption of sibling interactions, suggest that the father draws the juveniles' attention away from each other and their mother, and towards himself.

The results showed that, in the context of undisturbed family groups, body nosing among siblings increased in occurrence steadily from birth at least until the end of observations on post-natal day 46.

Forepaw-clasping by siblings and interactions in the venter-to-venter position sometimes accompanied body nosing: forepaw-clasping increased in frequency with age, but venter-to-venter interactions did not. These types of interaction involved some physical manoeuvering, such as pushing with the forepaws against the partner's shoulders in the mutual-upright position, and one animal achieving a physically superior position with respect to the other during forepaw-clasping. Both kinds of interaction may provide opportunities for some polarisation of inter-individual

relationships, perhaps on a dominant-subordinate axis.

When sibling young were removed from their home enclosure and placed in an unfamiliar one, they immediately began to display contact-promoting behaviour. However, the contact patterns observed lacked some components habitually seen on the part of young in their home enclosure: social grooming, venter-to-venter interactions and locomotor-rotational movements did not occur in this context. On the other hand, forepaw-clasping was more prominent than in the home enclosure. This appeared to be a contact behaviour and involved either neck or rump nosing. Further, neck nosing predominated over snout nosing in the unfamiliar enclosure, but not in the home cage. Since the odour of the neck seems to have attractive properties (Wilson, 1973; Wilson and Kleiman, 1974; Happold, 1976a), it is possible that the prominence of neck nosing is a response to an attractive and familiar stimulus in an otherwise unfamiliar situation.

When sibling dyads were observed in an unfamiliar enclosure, ♂♂ and ♂♀ dyads engaged in more body nosing and forepaw-clasping than did ♀♀ dyads. This suggests that males may respond more actively to disruption of or displacement from their social or physical environment.

Evidently there are different modes of contact-promoting behaviour in juvenile degus, including repetitious body nosing, forepaw-clasping, huddling, social grooming, venter-to-venter interactions and locomotor-rotational movements. The occurrence of these behaviours may sometimes overlap, and hence some of these

behaviours have been collectively termed 'play' (Wilson and Kleiman, 1974; Reynolds and Wright, 1979). The behaviours may in fact be differentially triggered, and should be clearly distinguished and interpreted in relation to the animals' ages and the social and physical context of observation.

CHAPTER FIVE

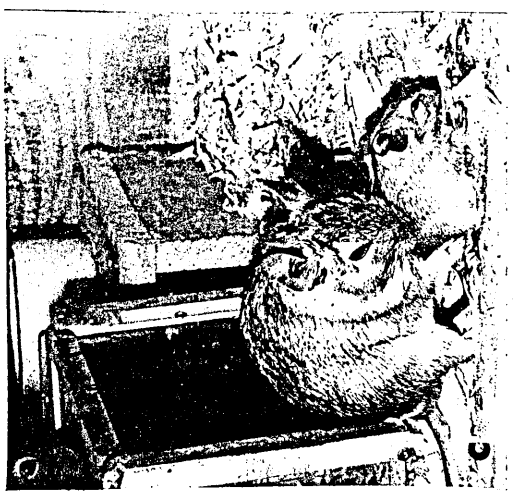
A COMPARISON BETWEEN TWO CAVIOMORPH RODENTS (*OCTODON DEGUS* AND *OCTODONTOMYS GLIROIDES*) OF JUVENILE SIBLING AND PARENT-YOUNG SOCIAL BEHAVIOUR.

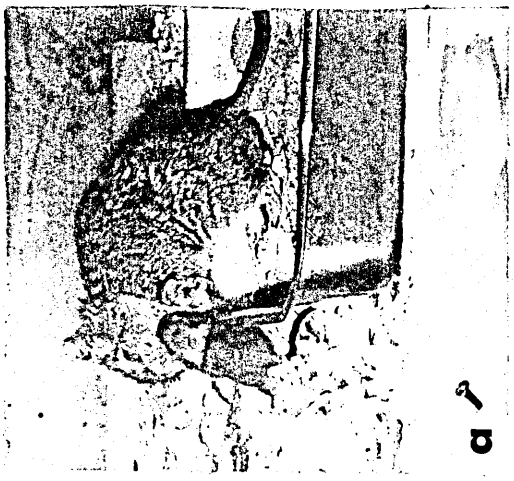
FRONTESPIECE

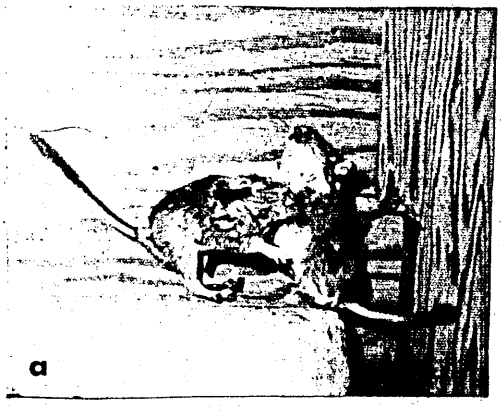
Interactions among young and other family members in Octodon and Octodonomys

Left: Interactions between Octodon infants and other members of and extended family group. (a) infant stretches up to make snout nosing contact with father; (b) juvenile from previous litter interacts with father, and infant attempts to join in; (c) Juvenile from previous litter noses infant's rump; (d) Nose-to-snout contact between infant and juvenile from previous litter; (e) venter-to-venter interaction in the mutual-upright position between infant and juvenile from previous litter.

Right: Interactions between Octodontomys littermates and between young and their mother. (a) jumping by young on left, and 'relaxed open mouth' by young on right (see also Fagen, 1981); (b) neck nosing; (c) young run around mother; (d) following a nosing contact one young writhes (with rotational movement) on the ground; (e) forepaw-clasping of young-to-mother young-to-young; (f) venter-to-venter interaction in the mutual-upright position; (g) venter-to-venter interaction in the supine-quadrupedal position - snout nosing; (h) venter-to venter interaction in the supine-quadrupedal position - neck nosing.



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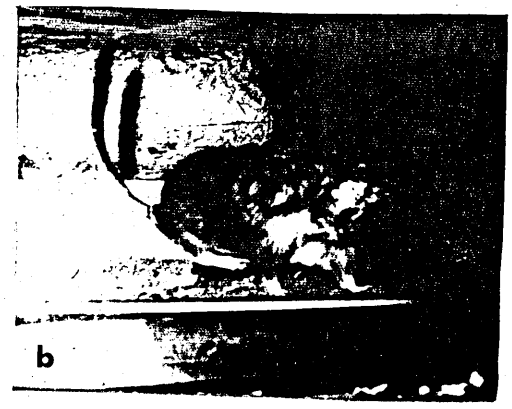
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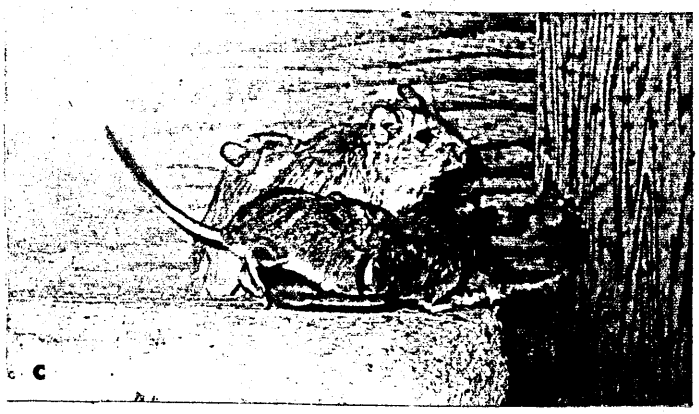
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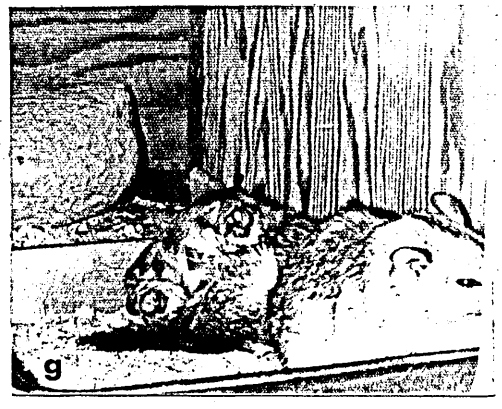
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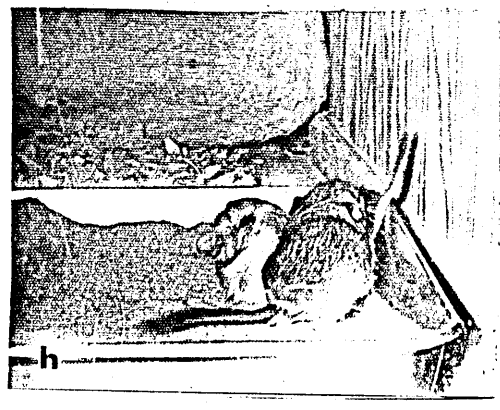
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ABSTRACT

Undisturbed family groups consisting of a litter and the mother or both parents of two caviomorph rodent species (Octodon degus and Octodontomys gliroides) in captivity were observed daily from the birth of the litter until the seventh week of age. Only non-aggressive and non-sexual behaviours were observed during this period; these behaviours were compared in the two species.

Octodon and Octodontomys were characterised from the literature of field observations and from the records of the captive colony at the National Zoo as being respectively more and less socially tolerant and communal. The Zoo records indicate that post-natal weight gain is slightly slower, and adult weight lower, in Octodontomys than in Octodon. Octodon undergo a change in temperament and pelage moult in the third month of age, whereas Octodontomys do not, and retain a relatively juvenile appearance into adulthood. The Octodontomys tail, however, develops a more prominent brush of hairs than in Octodon.

The behavioural observations indicated that Octodontomys infants were generally slightly more precocious than Octodon in the neonatal period, but thereafter were slightly slower to develop certain patterns of social behaviour characteristic of juveniles of both species. Octodon generally engaged in more

huddling, allogrooming, and forepaw-clasping than Octodontomys, and the Octodon father exercised social dominance over the young, which appeared not to occur in Octodontomys. Octodontomys engaged in more tail nosing, nibbling and pulling, more locomotor-rotational movements, and more parental participation in locomotor-rotational movements and venter-to-venter 'play' than occurred in Octodon.

These differences between the species are interpreted with reference to the different life histories of the socially tolerant Octodon and the less tolerant Octodontomys. However, the study concluded that there seemed to be no simple relation in these two caviomorph species between the degree of social tolerance and the overall amount of non-aggressive social interaction among siblings and between parents and young.

INTRODUCTION

In Chapter 4 the juvenile social development of the caviomorph rodent Octodon degus in captivity was described in some detail. The aim of the present chapter is to compare the occurrence of those social behaviour patterns of degu young and their parents already described with those of another Octodontid species, Octodontomys gliroides. This comparison was believed to be of interest because these two species exhibit contrasting lifestyles, Octodon being more communal, contact-prone and socially tolerant than Octodontomys (see below). This comparison therefore parallels, in some respects, the comparison of the socially tolerant prairie vole (Microtus ochrogaster) with the less tolerant meadow vole (M. pennsylvanicus) discussed in Chapters 2 and 3.

Free-living Octodon live in populous colonies which are divided into discrete communities (Fulk, 1976), whereas Octodontomys are sparsely distributed in nature (M. Shamberger, personal communication) and are probably semi-solitary in social habit. Octodon is a common small mammal of central Chile, occurring in low-lying grasslands in which animals use grass runways and shelter in underground burrows. Octodontomys occurs at higher altitudes in the montane regions of Chile and Bolivia, and its preferred habitat includes shrubs and rocky crevices in which the animals probably shelter (Walker, 1975).

The repertoire of visible behaviour acts of young and their parents is similar in both species (Wilson and Kleiman, 1974). This

repertoire includes exchanges of body nosing contacts, nibbling grooming movements, physical moanoeuvering in mutual-upright, supine-quadrupedal or forepaw-clasping positions, and bouts of leaping, running and head-shaking (locomotor-rotational movements). The superficial appearance of social interactions among family members in captivity differs in the two species in that (a) Octodon family members tend to huddle over one another when resting, whereas Octodontomys rarely huddle over one another, although they usually sleep side by side, (b) Octodontomys young tend to move more rapidly and energetically than Octodon during social interactions, which often build up to a faster tempo than in Octodon, and (c) Octodon tend to be more vocal than Octodontomys during non-aggressive interactions (Wilson and Kleiman, 1974; Reynolds and Wright, 1979).

In this chapter a quantitative comparison of juvenile and parent-young social behaviour characteristics observed in captivity will be presented. This will be preceded by a brief description of species differences in physical appearance and development. Subsequently, differences between the species in the occurrence of different behaviour patterns will be discussed in terms of the species' differing physical appearance and development, and social structure in nature, but their close phyletic relationship as Octodontids.

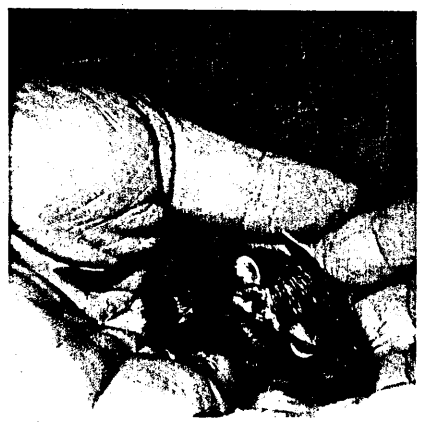
ANIMALS

Origin and maintenance The Octodon colony at the National Zoological Park was derived from four adults received in 1971 from a colony initiated in 1964 at the Massachussetts Institute of Technology. The Octodontomys colony was derived from three field-caught animals received in 1972. The young of both species together with their littermates and one or both parents inhabited spacious cages (100 x 60 x 50 cm) during this study. Pine shavings covered the floors, and each cage contained a nest box, a wooden block, a wooden platform and a sand tray. Dry food and fresh vegetables and fruit were fed daily, and water was always available. The place and conditions of captivity were as described for Octodon in Chapter 4.

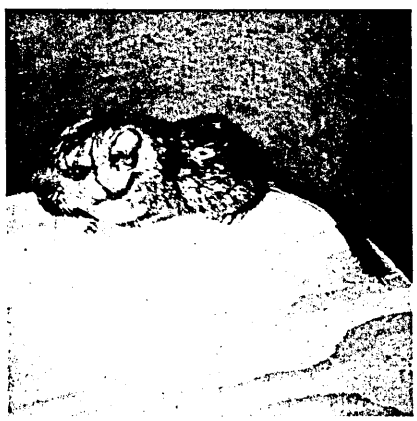
Reproduction and physical development The Octodon in the colony bred readily, but the long-term breeding success for Octodontomys was poorer. Although more docile than Octodon when handled, Octodontomys appeared more 'fragile' than Octodon, and occasionally exhibited signs of stress when confined with other conspecifics. Octodontomys had a longer gestation (105d) and smaller litter size (av. two young) than Octodon (87d and five young). Octodontomys young at birth were larger (av. 20g) than were Octodon neonates (av. 14g), but Octodon weighed more after the first week of age. Adult weights are around 200g and 190g for Octodon and Octodontomys respectively (Kleiman et al., 1980).

Figure 5.1

Physical characteristics during development of Octodontomys (left) and Octodon (right). (A) neonatal, (B) one month, and (C) two months (Octodontomys) and three months (Octodon). Photographs by E. Maliniak.



A



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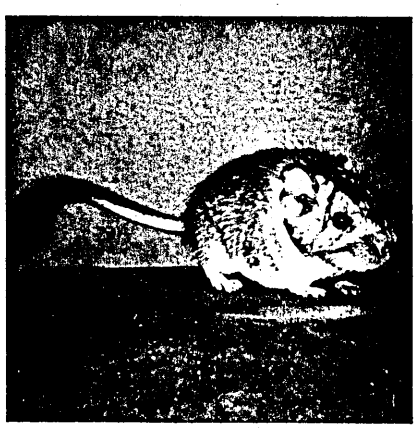


C

Both species were born with their eyes open and a dark neonatal pelage (Fig. 5.1a) which yielded during the first week to the gradual growth of a soft juvenile fur, which was pale brown in Octodon and grey in Octodontomys. In Octodon, the soft juvenile fur was gradually replaced during the third month of age by a more glossy, bristly coat; this coincided with a change in temperament, the young becoming more difficult to handle. The Octodontomys juvenile fur (Fig. 5.1 b, c) was retained into adulthood, and no change in temperament was noted. The rounded snout of juveniles of both species was retained into adulthood by Octodontomys, but acquired a more pointed appearance by the third month of age in Octodon (Fig. 5.1c). Octodontomys gradually developed a fuller brush of hairs at the tip of the tail than did Octodon (Fig. 5.1 b, c).

METHODS

The social behaviour of young with their parents in their home cage was recorded daily, in observation units of 15 min, from birth through the seventh week of age. The only difference in observation method for the two species was due to their natural difference in circadian rhythm, Octodon being primarily diurnal, alternating bursts of activity with rest periods, and Octodontomys being strictly nocturnal, with a peak activity period immediately after the onset of darkness. Octodon were therefore observed during the daytime, for two daily 15-min periods separated by at

least 2½h (as described in Chapter 4), while Octodontomys were observed by red bulb illumination for one or more 15-min bouts during the first hour of darkness. Ten litters of Octodon and four of Octodontomys were thus observed (Table 5.1). The 10 Octodon litters were the same as those of which the behaviour was discussed in Chapter 4; hence the father was present in five of the families, and absent in the other five. For two of the Octodontomys families the father was present, and for the other two he was absent.

Five of the Octodon and three of the Octodontomys litters were observed at the National Zoo, and the remainder in the basement of the author's home (see Chapter 4). Octodon observations totalled 211.25h, and Octodontomys 83.5h, that time being fairly evenly distributed over the seven-week observation period (Fig. 5.2). Fig. 5.2 indicates the range of body nosing scores per 15 min for Octodontomys compared with the mean scores per 15 min for Octodon (see also Chapter 4). The Octodontomys scores are presented separately for each litter because of the small number of litters and considerable inter-litter variation. No general effect of the father's presence on the amount of littermate interactions comparable to that found for Octodon (see Chapter 4) was suggested by these data. For the purpose of this chapter, data from all litters, regardless of the presence or absence of the father, are pooled when littermate or mother-young interactions are under consideration. For father-young interactions, only data from five Octodon and two Octodontomys litters are used.

Table 5.1. Number of families and individual parents observed.

	Octodon	Octodontomys
No. families observed in father's absence	5	2
No. different mothers involved	5	2
No. families observed in father's presence	5	2
No. different mothers involved	5	2
No. different fathers involved	4	2
No. individual mothers observed both in father's absence and presence	4	0
Mean litter size at parturition	5.6	3.0
(standard deviation)	(1.7)	(1.2)

A further three litters of Octodon and two of Octodontomys were observed from birth through the fourth week of age (at the National Zoo) in order to increase the number of litters for which the first appearance in ontogeny of juvenile behaviour patterns was recorded.

Notes on the behaviour of both species were handwritten, using a behaviour code. Nosing contacts by all family members were recorded, noting whether the nosing and nosed animal in each case was mother, father or young, and which of the following body target regions were nosed: snout, neck, rump, anogenital area and tail. Other body regions were infrequently nosed and have been excluded from this analysis. Most body nosing contacts were brief (i.e. less than two sec) and received a body nosing score of one. The nosing score was adjusted in the case of longer contacts; those lasting two sec or longer received a score of two. Allogrooming, in which an animal nibbled and licked another's fur, was also scored as two. However, prolonged unbroken bouts of allogrooming received a maximum nosing score of four (see also Chapters 3 and 4). The occurrence of selected behaviour patterns (allogrooming, interaction in the venter-to-venter position, forepaw-clasping, nosing in 'unstereotyped positions'— i.e. none of the foregoing contexts—and locomotor-rotational movements, including jumping, erratic running and head-shaking) was measured by an animal (mother, father or young) receiving a behaviour act score of one for a single performance of a behaviour pattern, regardless of duration. Thus the data for Octodon are identical to those analysed in Chapter 4, although they have been recast for the present analysis. The data for Octodontomys match those for Octodon as closely as possible.

RESULTS

First appearance in ontogeny of social behaviour patterns The age at which different components of juvenile behaviour were first performed by at least one infant of each litter during observation periods was noted (Table 5.2). The order of appearance was consistent among the different litters of each species (Kendall's coefficient of concordance, W = 0.69 for Octodon and 0.75 for Octodontomys, $P < 0.001$ in each case), and the order of appearance in ontogeny was the same for both species.

Octodontomys infants in the first week of age were initially slightly more precocious than Octodon in that they were first seen to leave the nest about one day earlier than Octodon, and to engage in neck nosing, snout nosing and jumping one to two days earlier (Table 5.2). This relative behavioural precocity of Octodontomys correlates with their longer gestation and heavier birth weight than Octodon (see ANIMALS section). The next behaviours to appear in ontogeny (head-shaking and interactions in the venter-to-venter position) were first seen at the same age in both species. This timing coincides with Octodon overtaking Octodontomys in weight gain. Tail nosing occurred at this age, but was only seen in Octodontomys. Forepaw-clasping was the last behaviour to appear in both species, and it was first seen significantly later in Octodontomys than in Octodon (Table 5.2).

Table 5.2. Age at which selected behaviours were first observed in Octodon and Octodontomys.

Behaviours	Octodon $\bar{X}$ age (days) for 13 litters	Octodontomys $\bar{X}$ age (days) for 6 litters	species difference (Mann-Whitney U test; two-tailed P)
	range	range	
leave nest	3.3 (3-5)	2.2 (1-4)	$P < 0.02$
nose-to-neck	3.9 (1-10)	1.8 (1-4)	$P < 0.02$
nose-to-snout	4.9 (3-8)	3.3 (1-9)	$P < 0.05$
jump	6.0 (3-14)	3.7 (1-7)	$P > 0.05$
head-shake	7.3 (3-13)	7.7 (1-14)	$P > 0.05$
nose-to-tail	-	8.7 (4-14)	
venter-to-venter	8.4 (6-13)	11.7 (2-21)	$P > 0.05$
forepaw-clasp	11.0 (5-15)	19.5 (11-27)	$P < 0.02$

Data distribution Fig. 5.2 indicates that the occurrence of body nosing among siblings increased from birth in both species. In Octodon this increase was found to have a linear relation with increasing age of the young throughout the first 46 post-natal days (Chapter 4). Examination of Fig. 5.2 for Octodontomys suggests that body nosing among siblings did not continue to increase with age past the fourth post-natal week in three of the four litters observed.

Fig. 5.3 indicates that overall the young of the two species displayed similar amounts of body nosing during observation periods. In more that 50% of observations of both species with young aged between 0 and 15 days there was no active social interaction recorded (the animals were resting or nursing). This percent of observations of total inactivity decreased as the young grew older, whereas the percentage of observation periods with per young nosing scores in the higher score ranges tended to increase. A greater tendency of young to interact with their parents in Octodontomys than in Octodon became evident after 30 days of age (Fig. 5.3).

Because of the species differences in activity rhythm (see ANIMALS section), a direct comparison of body nosing scores per unit time for each target region and behaviour act scores per unit time for each behaviour pattern would not be meaningful. Instead, the relative proportions with which different body regions were nosed, and with which different behaviour patterns occurred, are compared. In this way a picture may be obtained of the manner in which two related species with differing lifestyles combine the same behavioural elements in different proportions to produce two different mosaics characteristic of each species.

Figure 5.2

Ontogeny of body nosing scores for littermate interactions for 10 litters of Octodon and four of Octodontomys.

——— father absent; ------- father present.

The ordinate gives mean body nosing scores/young in litter/15 min for each 3-day period for Octodon and each 6-day period for Octodontomys.

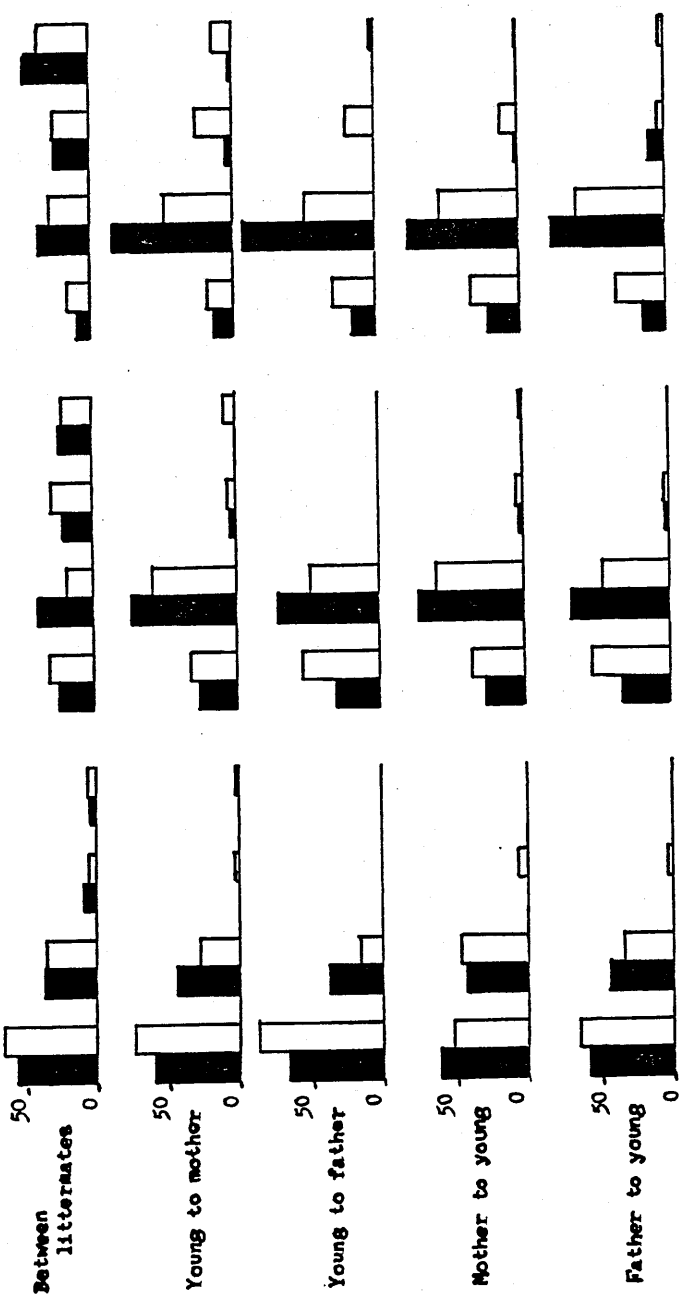
n = no. 15 min observation periods.

Octodontomys
n
18
14
10
6
2
1-6
7-12
13-18
19-24
25-30
31-36
37-42
42-48
2
3
5
7
Litter 7 5 2 3
f.a 18 18 18 18 18 18 18 18 18 18
f.a. 9 4 4 2 2 2 2 4 2 4
f.p. 15 14 15 12 9 12 9 2 9 6
f.p. 10 10 12 10 9 8 7

Octodon
Day
n
10
6
2
1-3
7-9
13-15
19-21
27-25
31-33
37-39
43-4
f.a. 28 28 30 30 28 30 30 26 28 28 26 28 28 26 30 30 21 26 34 33
f.p. 28 26 30 28 30 28 28 30 26 30 28 26 27 28 26 28 28 28 33

Figure 5.3

Distribution of body nosing scores for 15-min observation periods of family groups. s = score; shaded blocks = Octodon; unshaded = Octodontomys. No obs.: Octodon - 286, 279 and 280 for days 1-15, 16-30 and 31-46 respectively; Octodontomys - 121, 106 and 107 respectively for the same ages. Ordinate indicates % of observation periods yielding nosing scores in each score range indicated.


DAY 1-15
DAY 15-30
DAY 31-46
0
0<s<5
5≤s<10
s≥10
Between litternates
Young to mother
Young to father
Mother to young
Father to young
50
0

Species comparison of behaviour repertoire Since the data for each class of interactants (littermate, mother-to-young, etc.) have been pooled for all ages and all litter groups, cross-tabulation of the data was undertaken in order to explore ways in which the general picture presented for each species (Figs. 5.4 and 5.5) might be further qualified by knowledge of the range of proportions of nosing of the different body regions and of the different behaviour patterns according to litter, and any obvious deviations from this general picture by the three different age groups.

For both species the greatest amount of nosing was directed towards the anterior end of the body, i.e. the snout and neck regions. The anogenital region was nosed very little (Fig. 5.4).

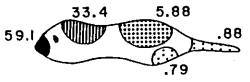
There were some differences between the species concerning the % snout nosing of the total nosing scores. The % snout nosing was generally greater in Octodon than in Octodontomys (Fig. 5.4). Amongst littermates the % snout nosing ranged in different litters from 49.5% to 65.5% in Octodon compared with 39.1% to 52.8% in Octodontomys ($U = 2$, 2-tailed $P < 0.02$, Mann-Whitney U test). For young nosing the mother, the % snout nosing ranged in different litters from 27.5% to 61.1% in Octodon and 13.6% to 28.8% in Octodontomys ($U = 1$, $P < 0.02$), but for young nosing the father the species did not differ (Octodon range 23.6% to 67.1%, Octodontomys litters 23.6% and 49.8%; $U = 2$, $P = 0.38$). For neither mother-to-young nor father-to-young nosing did the species differ (mother-to-young Octodon range in different litters was 36.1% to 75.8%, Octodontomys range 40.0% to 46.9%, $U = 10$, $P = 0.10$;

Fig. 5.4

The proportions with which each of five body regions were nosed in Octodon and Octodontomys.
The five body regions shaded in the figure are referred to in the text as snout, neck, rump, anogenital and tail. The unshaded body area in the figure is the area which was seldom the target of nosing contacts. Occasional nosing of this area was excluded from the total nosing scores (n) given in the figure.
n = total body nosing score, pooled from all observations of all litters, for each class of interactants.

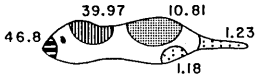
OCTODON

Between littermates



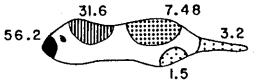
n = 22959

Young nosing mother



n = 3615

Young nosing father

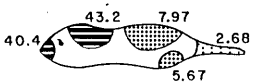


n = 2060

Mother nosing young

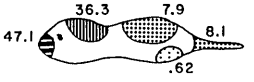
n = 3514

Father nosing young

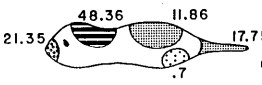


n = 2947

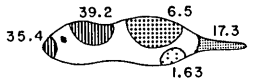
OCTODONTOMYS



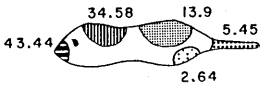
n = 4715



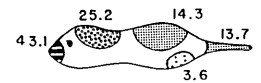
n = 2120



n = 429



n = 1005



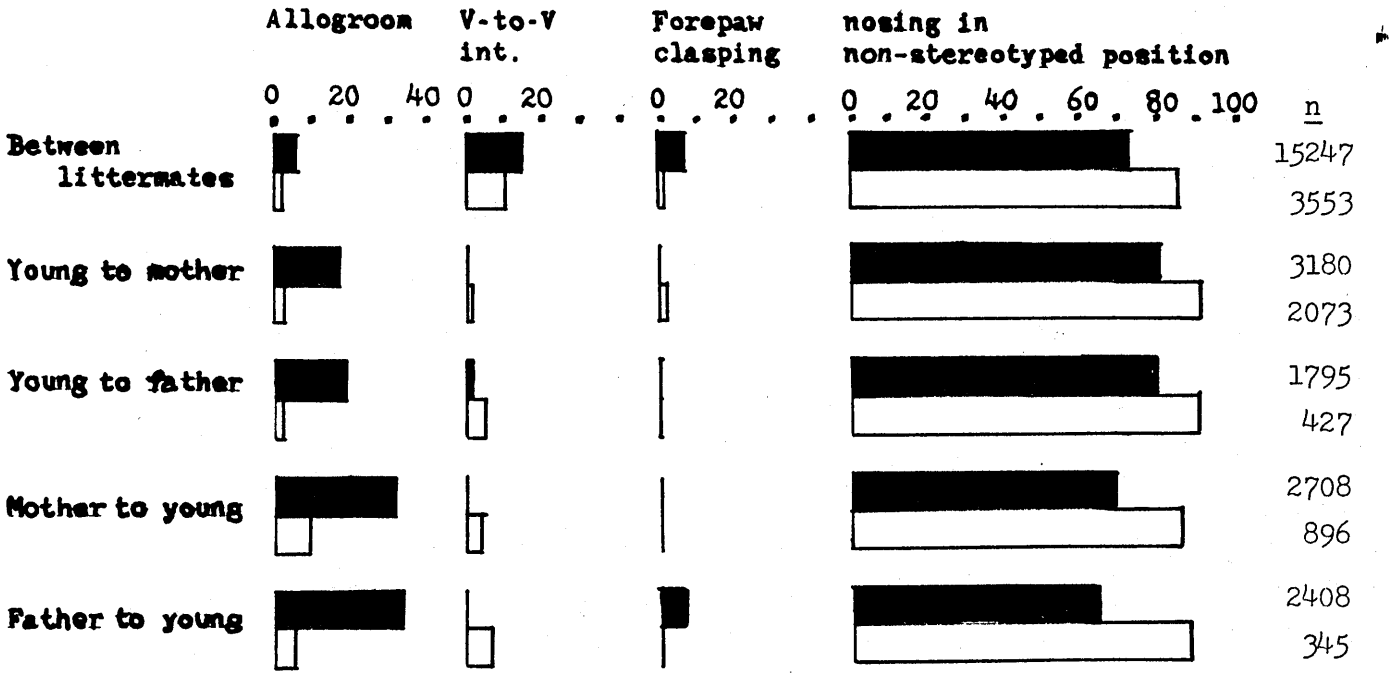
n = 357

%

- > 0 ≤ 5
- > 5 ≤ 10
- > 10 ≤ 20
- > 20 ≤ 30
- > 30 ≤ 40
- > 40 ≤ 50
- > 50 ≤ 60

Fig. 5.5

The proportions with which each of four types of behaviour occurred in Octodon and Octodontomys.
The four behaviour patterns considered here are allogrooming, venter-to-venter interactions, forepaw clasping, and body nosing in non-stereotyped positions. The blocks give the % contribution, in terms of behaviour act scores, of each behaviour pattern to the total (n).
n = the total behaviour act score for these four behaviour patterns pooled from all observations of all litters, for each class of interactants.
Shaded blocks = Octodon; unshaded blocks = Octodontomys.


Allogroom
V-to-V int.
Forepaw clasping
nosing in non-stereotyped position
0 20 40
0 20
0 20
0 20 40 60 80 100
n
Between littermates
15247
3553
Young to mother
3180
2073
Young to father
1795
427
Mother to young
2708
896
Father to young
2408
345

father-to-young Octodon range 30.4% to 50.6%, Octodontomys litters 33.6% and 52.0%; U = 6, $P > 0.90$). Thus the species difference was most evident in the behaviour of young towards each other and towards their mother than in the behaviour of adults.

In Octodon there was no difference between the three age groups in the proportions with which the different body regions were nosed during interactions among littermates or between parents and young. However, for Octodontomys mothers nosing their young, the % snout nosing increased from 27.2% of the total nosing score during days 1-15 to 46.9% during days 16-30, and to 51.2% during days 31-48. For Octodontomys fathers nosing the young, the % snout nosing of the total for the same ages were 13.9%, 39.8% and 56.5% respectively. The % neck nosing by both parents to the young correspondingly declined with age. Conversely, for Octodontomys young nosing their mother, the % neck nosing of the total nosing score increased with age (24.3%, 47.3% and 53.3% respectively for the three age groups); this might be related to a tendency noted for Octodontomys young to perch on their mother's back while repeatedly nosing her neck and head-shaking. There was no obvious change with age in the % snout or neck nosing for Octodontomys young nosing their father, or for nosing among littermates.

Octodontomys generally nosed the tail more in proportion to the other body regions than did Octodon (Fig. 5.4). When the different litters were considered, the % tail nosing of the total nosing scores for sibling interactions ranged from 6.6% to 11.3% in Octodontomys compared with 0.2% to 2.3% in Octodon (U = 0, $P < 0.002$,

Mann-Whitney U test. For nosing contacts by the young to the parents, the % tail nosing of the total nosing score ranged from 10.9% to 33.2% in Octodontomys compared with 0.7% to 6.4% in Octodon (U = 0, P = 0.002), and the % tail nosing of the father by the young was 16.1% and 17.7% in the two Octodontomys litters compared with a range of 1.7% to 4.1% in Octodon (insufficient Octodontomys data for a significant P value by the Mann-Whitney U test). When parental nosing of the young was considered, the species did not differ significantly when the % tail nosing of the total nosing for each litter was compared. Thus, as for snout nosing, the species difference in tail nosing was found more in the behaviour of the young than in the behaviour of their parents. With respect to tail nosing, this may be due in part to the relatively greater development of the tail brush of hairs in Octodontomys adults than in the young, and in part to the relatively greater activity level of the young with respect to their parents than the reverse. The pursuit, nosing, nibbling and pulling of their parents' tails by young Octodontomys was often an integral part of play bouts (Wilson and Kleiman, 1974). The % tail nosing of nosing scores of the young did not differ in the three age groups, but the % tail nosing of the young by the parents did increase with age of the young (1.6%, 4.5% and 6.9% for mother-to-young nosing in the three age groups, and 4.6%, 10.8% and 13.0% for father-to-young nosing). Possibly this increase is related to the gradual development of the hair brush from infancy onwards.

No consistent differences between the species occurred

Mann-Whitney U test. For nosing contacts by the young to the parents, the % tail nosing of the total nosing score ranged from 10.9% to 33.2% in Octodontomys compared with 0.7% to 6.4% in Octodon ($U = 0$, $P = 0.002$), and the % tail nosing of the father by the young was 16.1% and 17.7% in the two Octodontomys litters compared with a range of 1.7% to 4.1% in Octodon (insufficient Octodontomys data for a significant P value by the Mann-Whitney U test). When parental nosing of the young was considered, the species did not differ significantly when the % tail nosing of the total nosing for each litter was compared. Thus, as for snout nosing, the species difference in tail nosing was found more in the behaviour of the young than in the behaviour of their parents. With respect to tail nosing, this may be due in part to the relatively greater development of the tail brush of hairs in Octodontomys adults than in the young, and in part to the relatively greater activity level of the young with respect to their parents than the reverse. The pursuit, nosing, nibbling and pulling of their parents' tails by young Octodontomys was often an integral part of play bouts (Wilson and Kleiman, 1974). The % tail nosing of nosing scores of the young did not differ in the three age groups, but the % tail nosing of the young by the parents did increase with age of the young (1.6%, 4.5% and 6.9% for mother-to-young nosing in the three age groups, and 4.6%, 10.8% and 13.0% for father-to-young nosing). Possibly this increase is related to the gradual development of the hair brush from infancy onwards.

No consistent differences between the species occurred

in the proportion of nosing directed to the rump and anogenital regions. However, there was a tendency in Octodontomys for the % rump nosing by parents towards their young to decrease during juvenile development (18.3%, 15.9% and 1.9% for mother-to-young in the three age groups, and 26.2%, 20.5% and 10.4% for father-to-young).

Fig. 5.5 presents a summary of the species comparison with respect to the occurrence of allogrooming, interactions in the venter-to-venter position, forepaw-clasping, and nosing outside of these contexts (in 'unstereotyped positions').

Octodon generally engaged in more allogrooming in proportion to other behaviour patterns than did Octodontomys (Fig. 5.5). When the different litters were considered, the % allogrooming of mother-to-young behaviour acts ranged from 15.0% to 47.8% in Octodon compared with 6.3% to 14.4% in Octodontomys ($U = 0$, $P = 0.002$), and the % allogrooming of father-to-young behaviour acts ranged from 20.5% to 34.9% in Octodon compared with 3.9% and 7.5% in the two Octodontomys litters (insufficient Octodontomys data for a significant P value by the Mann-Whitney U test). For littermate interactions the % allogrooming ranged in different litters from 1.4% to 13.6% in Octodon compared with 1.0% - 4.2% in Octodontomys ($U = 4$, $P = 0.05$). The species were similar, however, in that the lowest figure for allogrooming as a percentage of the total behaviour act scores was for littermate interactions, and the highest was for the behaviour of parents towards their young (Fig. 5.5).

Forepaw-clasping occurred relatively more in Octodon than in Octodontomys (Fig. 5.5). Amongst littermates, Octodon engaged

did not decrease in Octodon (23.0%, 32.0% and 32.5% respectively). In Octodon there was an increase in the % forepaw-clasping of the young by the father (0.0%, 5.7% and 8.7% in the three age groups). In Octodontomys the % venter-to-venter interactions of parent-to-young behaviour act scores increased slightly with increasing age of the young (0.0%, 2.2% and 10.8% for father-to-young behaviour, and 2.8%, 2.5% and 5.4% for mother-to-young behaviour).

The species difference in the extent to which locomotor-rotational movements occurred was considered separately from the behaviour patterns discussed above, since the latter are contact behaviours, and contact behaviours tended to be interrupted by locomotor-rotational movements (Wilson and Kleiman, 1974). Locomotor-rotational movements are considered here in terms of the ratio of their scores to body nosing scores, in order to portray the general extent to which social interactions were punctuated by these movements in the two species (Table 5.3; body nosing scores from allogrooming have been deducted from the total scores given here, since allogrooming usually occurred at the start of rest periods, and was seldom accompanied by locomotor-rotational movements in either species).

It is clear from table 5.3 that Octodontomys young generally engaged in more locomotor-rotational movements in relations to body nosing scores than did Octodon young. When the different litters were considered, the ratio ranged from 0.3

Table 5.3. The ratio of behaviour act scores for locomotor-rotational movements to body nosing scores (excluding allogrooming).

	l-r movs/body nosing	
	Octodon	Octodontomys
between littermates	0.101	0.586
young to mother	0.070	0.401
young to father	0.058	0.599
mother to young	0.002	0.144
father to young	0.005	0.135

to 0.9 in Octodontomys compared with 0.04 to 0.16 in Octodon ($U = 0$, $P = 0.002$ by the Mann-Whitney U test). It is also evident from Table 5.3 that whereas Octodon parents almost never joined with their young in these movements, Octodontomys parents sometimes did. When the different Octodontomys litters were considered, the ratio of locomotor-rotational movements to body nosing scores ranged from 0.00 to 0.36 for mother-to-young behaviour, and was 0.03 and 0.24 for the behaviour of the two fathers. Consideration of ratios for the different Octodon litters was inappropriate, since locomotor-rotational movements by the parents hardly ever occurred.

The ratio of locomotor-rotational movements to body nosing scores for littermate interactions decreased with age in both species. For Octodontomys young the ratios in the three successive age groups were 0.81, 0.51 and 0.44, and for Octodon the comparable ratios were 0.15, 0.10 and 0.06 respectively. Thus it appears that young of both species may become progressively less likely to engage in locomotor-rotational movements during body nosing interactions as they grow older.

DISCUSSION

The behaviour of Octodon degus and Octodontomys gliroides described in this chapter encompasses all the juvenile and parent-young social behaviour observed to occur within the limits of the study conditions with the exception of vocalisations, nosing the mouth of an eating animal, and behaviour involving urination and sandbathing (Wilson and Kleiman, 1974; Kleiman, 1975; Reynolds and Wright, 1979). In this study it has been found that litters of the two species raised and observed in captivity differed in (a) the pace of social behaviour ontogeny, (b) the relative amounts of tail and snout nosing during sibling and parent-young interactions, and (c) the relative prominence of the following non-aggressive and non-sexual behaviours: allogrooming, forepaw-clasping, venter-to-venter 'play' between parents and young, and locomotor-rotational movements. Possible correlations between these observed species differences in behaviour and known or presumed differences between the species in life history will now be considered.

Octodontomys neonates were slightly larger and behaviourally more precocious than Octodon infants, but post-natal development in Octodon was more rapid. Furthermore, Octodon young in the third month of age undergo physical and behavioural changes away from the juvenile form, whereas Octodontomys retain into adulthood their juvenile appearance and behavioural features such as locomotor-rotational movements and venter-to-venter 'play'.

There are, therefore, two aspects of behavioural contrast in the two species with which this discussion is concerned. One aspect is the greater social tolerance of Octodon relative to Octodontomys, and the other is the afore-mentioned similarity of adults and juveniles in Octodontomys compared with the relatively greater physical and behavioural disparity between adults and juveniles in Octodon.

With respect to nosing different parts of the body, the two species differed mainly in that Octodontomys nosed the tail relatively more than Octodon; this difference is undoubtedly associated with the greater amount of hair at the tip of the tail in Octodontomys than in Octodon. A possible interpretation of tail nosing in Octodontomys is that it may be a mode of olfactory exchange which does not necessitate close body contact: individuals may nose each other while keeping 'a tail's length' apart. Since Octodontomys also differed from Octodon in tending to nose the snout relatively less, it is possible that tail nosing may be partly substituting for snout nosing.

With respect to the different behaviour patterns observed, the species differed in the relative emphases afforded to each pattern. Octodon engaged in relatively more allogrooming than Octodontomys. Octodon usually huddle over one another when resting, and allogrooming is often a prelude to huddling. Octodontomys, other than parents with young infants, rarely huddle over one another. Thus allogrooming may be considered to be a contact-promoting behaviour which is, not surprisingly, more prevalent in Octodon than in Octodontomys.

Octodontomys, both young and parents, displayed a greater incidence than Octodon of locomotor-rotational movements in proportion to body nosing scores. It is possible that locomotor-rotational movements function to control the intensity of olfactory and tactile stimulation to the interactants by continually causing the animals to break contact. By punctuating social interaction with these movements, therefore, contact may be made repeatedly in a relatively contact-shy species such as Octodontomys without stressful levels of stimulation being reached (Kleiman, 1974; Golani, 1976). It is also possible that the high level of locomotor-rotational movements in Octodontomys is related to their circadian rhythm; Fagen (1976) suggested that physically energetic social interaction may be predicted after a period of confinement (Octodontomys sleep all day), and may be beneficial physiologically as a warm-up before starting to forage. Our Octodontomys rarely ate the fresh food provided daily until long after their initial evening period of intense social interaction. There are, therefore, two contrasting points to be noted here: firstly, Octodontomys, the more contact-shy species, engaged in more locomotor-rotational movements than Octodon, and secondly, these energetic movements, which appear playful, are considered to be characteristic of young animals of both species, but also occur to a considerable extent in adult Octodontomys, but not Octodon.

Interactions in the venter-to-venter position occurred

between parents and young in Octodontomys but not in Octodon. These interactions are usually accompanied by locomotor-rotational movements in Octodontomys and the gurgling vocalisation in Octodon, and appear playful in both species. Participation by Octodontomys parents in these interactions may be linked to their participation in locomotor-rotational movements; Octodon parents participated in neither. During venter-to-venter interactions between sibling young of both species, the partners appeared to be attempting to match rather than to exceed each other's manoeuvres. Possibly such reciprocal matching of physical skills may be inappropriate to a dominant-subordinate relationship such as seems to develop between Octodon parents (especially the male) and their young (Chapter 4), but may be appropriate for parent-young interactions in Octodontomys, in which species a behavioural 'generation gap' seems not to occur.

The occurrence of paternal forepaw-clasping was greater in Octodon than in Octodontomys. Forepaw-clasping of the young by the Octodon father appeared to be associated with paternal control of the young; among sibling juvenile Octodon it appeared to be primarily a contact-promoting behaviour (Chapter 4). Probably these two functions of forepaw-clasping are not clearly separable at any age in Octodon. The lesser emphasis on this behaviour in Octodontomys may reflect the lesser degree of contact-proneness in this species, and the lack of social dominance exercised by the male parent.

In regard to paternal socio-sexual domination of the young in Octodon in contrast to Octodontomys, an exerpt from the behavioural records of one family of each species observed into the litter's third month of age are of interest:

> The Octodon father (♂#4) often forepaw-clasped his son when the son engaged in venter-to-venter interaction with one of his sisters, or attempted to forepaw-clasp her. The father would rush up to the son, clasp him with pelvic thrusting and without the gurgling vocalisation, and would continue to hold him for some time.
>
> When the young were 2.5m old, the mother entered oestrous. The father proceeded to intimidate his son by threatening him with the sideways presentation posture and by fighting him (see Davis, 1975). He left his son alone only for as long as the son remained frozen in a hunched 'rump-raised' position. He would then approach the son periodically and 'toss' him posterio-ventrally with the snout, urinate on him, lean over him and allogroom him. The son had to remain immobile to avoid being attacked. Later that day the father successfully copulated with the mother. He then discontinued his severe intimidation of his son.

> By contrast, when Octodontomys litter #2 was 2.0m old, the mother entered oestrous. The father displayed intense courtship behaviour towards her for two days, but did not threaten his son, or attempt to limit his movements in any way.

Thus certain linkages between some behavioural traits found to be emphasised by each of the two species are suggested, as follows: Octodon: contact-proneness, communal multi-male groups in nature, huddling, allogrooming, forepaw-clasping, loss of juvenile play behaviours in adults, and finely controlled socio-sexual domination of the young by the breeding male; Octodontomys: limited social tolerance, semi-solitary dispersed lifestyle in nature, development of tail hairs and

tail nosing, locomotor-rotational movements, juvenile physical appearance and play behaviour retained in adult, absence of controlled dominance behaviour from parent to young. Further observations of other caviomorph species will be necessary to test the strength of these linkages. Despite the fact that Octodon is known to be more contact-prone than Octodontomys, this study has shown that it would be misleading to describe Octodon as being more 'interactive' or 'playful' than Octodontomys; in these species there does not seem to be any simple relation between the degree of social tolerance and the amount of social interaction. This conclusion is in keeping with the view of Kleiman (1974) that caviomorphs are able to live in close association with conspecifics "...regardless of the niche they occupy or the complexity of the social system."

The concept of defining species characteristics in terms of non-aggressive and non-sexual behaviours of young animals is still relatively new (Bekoff, 1974; Happold, 1976; see also Chapter 3). It is hoped that the results of the present chapter may be stimulating to this field of endeavour.

CHAPTER SIX

COMPARATIVE DISCUSSION

Although the overt behaviours contributing to juvenile socialisation are similar in the four rodent species discussed in this thesis, I found differences between the more and less socially tolerant and communal species of each of these two types of rodent, microtine and caviomorph, in the level of occurrence of certain social behaviours. These behaviours included body nosing and 'play' patterns, sitting in contact, huddling and allogrooming, and parent-young contact. The direction of the difference between the more and less socially tolerant species in some of these behaviours (such as sitting in contact, huddling and allogrooming, and father-young contact, which all occurred to a greater extent in the more socially tolerant and communal species) was the same in the Microtus and the Octodontids. In this comparative discussion I will summarise the similarities found between the Microtus and the Octodontids in the contrast between the more and less tolerant and communal types with respect to these behaviours. To ease the repetition of words in this discussion, I will refer throughout to Microtus ochrogaster and Octodon degus as the TOL (more tolerant and communal) species, and to Microtus pennsylvanicus and Octodontomys gliroides as the INT (less tolerant and less communal) species.

Besides these similarities in the manner in which juvenile behaviours may relate to social tolerance and social structure in the Microtus and Octodontids, some differences between the two rodent types were found with respect to certain behaviours that may relate to the difference between the two Microtus and two Octodontid species in their physical attributes. The Microtus are small rodents

with an approximate adult weight of 30g, life span of one year, and gestation of three weeks, in contrast to the Octodontids with an approximate adult weight of 200-250g, life span of five years, and gestation of three months. The behaviour discussed in this respect includes the form and use of rotational movement and physical manoeuvering during play, the frequency of spontaneous social interaction in family groups, and the use of autogrooming during social interactions. Although these aspects of behaviour were not all central to the separate discussions of Microtus and Octodontid juvenile socialisation (Chapters 2, 3, 4 and 5), it is thought that they may relate to major differences in central nervous organisation and the behavioural basis of social organisation in these two rodent types.

In this comparative discussion I will consider first the behavioural differences between the species which correlate with known differences in social tolerance and communality, and then I will consider the behavioural differences between the species which relate to differences in the physical type of rodent, as discussed above. Earlier chapters will be referred to for material already presented in this thesis, and some supplementary material will also be incorporated here.

Both TOL species were found to exceed both INT species in the level of occurrence of certain behaviour patterns during family social behaviour, as discussed in Chapters 2, 3 and 5. The TOL fathers displayed much enthusiasm for the young, and squatted or huddled over them for much of the time when compared with the INT fathers. The TOL fathers huddled over their mates (see Thomas and Birney, 1979, for an illustration of this behaviour in M. ochrogaster), whereas INT fathers rarely did. In the TOL species there was more allogrooming than in the INT species. In Microtus, the TOL mothers spent more time than the INT mothers in contact with their young, but a similar comparison could not be made in the Octodontids because of the difference between the two octodontid species in activity rhythm. However, in both types of rodent I found that the young of the TOL species generally received greater exposure to conspecific tactile and olfactory stimuli during the settling and inactive phases of their activity cycle.

During activity periods stimulated by the dyadic encounter procedure, juvenile interactions between sibling and non-sibling voles resulted in higher body nosing scores in the TOL M. ochrogaster than in the INT M. pennsylvanicus (Chapter 3). Comparable data on the Octodontids have not been included in Chapter 5 owing to the limited availability of young animals, and hence the lack of emphasis on dyadic encounters in the Octodontid study (see Chapters 1 and 4). However, a small amount of data obtained from 17 Octodontomys sibling encounters

(9 ♂♀ and 8 ♀♀ encounters evenly distributed over weeks 2 to 7, using animals from five litters) and 24 comparable Octodon sibling encounters (12 ♂♀ and 12 ♀♀ encounters, using animals from six litters; these Octodon encounters are the same as those described in Chapter 4, but the ♂♂ dyads have been eliminated here in order to make the encounters more comparable with those of Octodontomys) suggested that the number of body nosing contacts was generally lower in the INT Octodontomys ($\bar{X}$ = 33.8 nosing contacts, range 13 to 47) than in the TOL Octodon ($\bar{X}$ = 56.0, range 10 to 116; $P < 0.001$ by the Mann-Whitney U test). Thus in both the Microtus and the Octodontids, the TOL species were found to engage in more body nosing during sibling encounters than were the INT species (although it must be emphasised that this conclusion is very tentative for the Octodontids, being based on only a small number of encounters); the exposure of juveniles to tactile and olfactory stimuli from their encounter partners was therefore presumably greater in both TOL species than in the INT species.

A comparison was made between the TOL and the INT species of 'play' behaviour (termed Mode II interactions in the vole study, Chapter 3). In all species, dyadic play interactions (from approach to separation) which included locomotor-rotational movements or physical manoeuvering combined with relaxed muscle tone or open mouth, could be readily identified and isolated from the complete body nosing record for the purpose of species comparison of these specifically play behaviour episodes.

Rotational head movement accompanied body nosing during Mode II interactions of both Microtus species; this was a rapid lateral rocking movement of the head during which the snout formed a fixed point of contact with the other animal, thus becoming a pivot for the head rotation. It seems likely that the potential for olfactory input may be enhanced by head-rocking while the snout is buried in the companion's fur. About 60% of all TOL M. ochrogaster Mode II interactions included further head rocking following the initial occurrence, compared with about 30% in the INT M. pennsylvanicus: possibly the INT species has a lower tolerance for such enhanced olfactory input. In the Octodontids the rotational head movement differed in quality from that of the Microtus; instead of a rocking movement with the snout as a pivot, the movement resembled more a shake or toss, resulting in interruption of the snout-body contact. Thus head-shaking was (as described in Chapter 5) more frequent in the INT Octodontomys than in the TOL Octodon. In all four species the rotational head movement conveys to the observer, and probably also to the animals, the message "this is play" (Bateson, 1956; Bekoff, 1974; Wilson and Kleiman, 1974).

When rotational head movements of the TOL M. ochrogaster and Octodon were compared, it was evident that head-rocking in M. ochrogaster was a more effective contact-promoting signal than was head-shaking in Octodon: 45% of instances of head-shaking were immediately followed by further nosing in one typical litter of Octodon (Wilson and Kleiman, 1974) compared with 85% of instances of head-rocking in M. ochrogaster. Further, since 70% of instances

of reciprocal behaviour acts (venter-to-venter manoeuvering or reciprocal nosing of the head or rump) in M. ochrogaster were accompanied by head-rocking, this movement might be interpreted as a contagious signal acting to coordinate reciprocal movement in this species. Thus it seems that rotational head movement - which is a common 'play signal' in mammals (Wilson and Kleiman, 1974) - may vary somewhat in precise form and function in different taxonomic groups.

Some observed behavioural differences between the microtines and the Octodontids may relate to the probable greater ability of the Octodontids to learn and remember physical and behavioural characteristics of individual conspecifics, and use this information in the development of complex and durable social relationships during their relatively long lifespan. Davis (1975) has shown that male Octodon can remember individual identity and behavioural characteristics for at least a month after a single encounter. The present study indicated that physical manoeuvering occurred more often in Octodon than in M. ochrogaster, that spontaneous interaction levels among siblings were much greater in Octodon than in M. ochrogaster, and that Microtus individuals in dyadic encounters involved autogrooming apparently at least in part to clarify the difference between the two animals in individual odours. These differences will be detailed below.

Physical manoeuvering (in the mutual-upright, supine-quadrupedal and forepaw-clasping positions) during 157 play

(Mode II) interactions taken from family group observations of two typical litters of Octodon and from dyadic encounters of M. ochrogaster was compared in these two species. One such manoeuvre initiated the play interaction in 82% of cases in Octodon, but only 16% in M. ochrogaster; in Octodon, 21% of play interactions included three or more occurrences of manoeuvering compared with only 2% in M. ochrogaster. In Chapter 4 I suggested that these kinds of manoeuvres in Octodon might provide opportunities for polarisation of inter-individual relationships, perhaps on a dominant-subordinate axis, those animals with the greater manoeuvering ability becoming relatively dominant with respect to their peers. The low incidence of these manoeuvres in M. ochrogaster may indicate that inter-individual differentiation on the basis of manoeuvering ability occurs little or not at all. A few observations of stable extended family groups of both species suggest the presence of behavioural dominance in Octodon (Chapter 5), but not in M. ochrogaster (unpublished observations). Physiological dominance of the breeding pair occurs in M. ochrogaster, with grown young remaining in the parental group being physiologically immature (Batzli et al., 1979; Chapter 3). All such non-reproducing voles probably remain socially 'equal' and behaviourally undifferentiated. In the voles, the physiological mechanism, thought to be mediated by pheromones, is probably analagous to the Octodon system of behavioural dominance, which undoubtedly requires complex learning and memory processes.

In undisturbed family groups the littermate body nosing scores peaked for M. ochrogaster at less than one per infant per

15 min in the third week of age (Chapter 2) compared with the equivalent Octodon scores of about 5 in the third week of age rising to twice that level by the seventh week of age (Fig. 4.2). Thus in Octodon the presence of familiar littermates in the home enclosure seems to be a sufficient stimulus for social interaction, whereas in Microtus this situation seems to be insufficient. However, since mean body nosing scores per sibling dyadic encounter were of the same order of magnitude in M. ochrogaster and Octodon (averaging around 50 per dyad in both species), the difference between these two species cannot be a difference in ability to engage in social interaction with family members, but may be a difference in 'arousal' (Barnett, 1963) within the undisturbed family group. This species difference in spontaneous interaction levels may correlate with the presumed greater need in Octodon than in Microtus for continual social interaction in the development of complex social relationships within the family group.

In dyadic encounters of both Microtus species, autogrooming tended to occur most frequently at the start of encounters, before the animals made their initial approach to each other and also during their first minutes of investigation. The three body regions intensively autogroomed were the same as those habitually nosed during social interactions. A vole would rub the angle of the mouth with the forepaws and then wipe its paws over the nostrils. After rubbing the paws over the back of the head and neck, they would again be wiped over the nostrils. The neck - and less often

the mouth and rump - was sometimes scratched with the toes of the hind foot, and the toes were then chewed. Voles presumably renewed knowledge of their own odours during autogrooming; hence the opportunity existed for an autogrooming vole to compare its own odours with those of the other animal by then nosing the other animal. The dyad could then exchange information on whether they were siblings or non-siblings, and of the same or different sex. No long-term memorising would be required for such a mechanism. Thiessen and his colleagues (1976; 1977) have found that a social attractant is actually released by autogooming during encounters between gerbils (Meriones unguiculatus), another cricetid rodent. This kind of autogrooming did not occur during the octodontid dyadic encounters; presumably these animals place more reliance on learning and memorising conspecifics' individual characteristics, as discussed above.

These behavioural differences between the Microtus and the Octodontids occurred within the limits of this study; the interpretations of them, discussed above, are conjectural, although they all relate to the relatively longer life-span, low turn-over of individuals, and probably greater ability for complex learning and long-term memorising in the octodontids when compared to the Microtus. Caution should be exercised in generalising from these results and interpretations beyond the species of this study, since it is likely that some differences between species due to phylogenetic origin may be obscured by

other differences in phylogeny and ecology. For example, the dwarf mara (Pediolagus salinicola) is a caviomorph which, unlike Octodon and Octodontomys, does not engage in physical manoeuvering play in family groups (Wilson and Kleiman, 1974). Studies of many more species are needed before generalisations may become useful.

CHAPTER SEVEN

CONCLUSIONS

In this study attention has been focussed on the behaviour of young and their parents of two microtine and two octodontid rodent species while the animals engage in body contact and interact non-aggressively.

Although the documenting of a difference between the more and less socially tolerant ('TOL' and 'INT' respectively; see Chapter 6) species in the amount of parent-young contact and body nosing behaviours among juveniles was predicted, and was hardly surprising, it is the magnitude of the species differences which will be of interest when this kind of study is extended to other species in the search for correlations between aspects of juvenile and parent-young behaviour and social structure. Although in this study two pairs of related species with contrasting social structures were compared, the contrast in juvenile and parent-young behaviour scores was far from extreme: in fact all four species displayed considerable parent-young contact and body nosing behaviours. Particularly in the case of the voles, juvenile dyads of the two species could seldom be distinguished on the basis of individual encounters, and the accumulation of many observations was necessary before a numerical difference between the species in behaviour scores became clearly apparent. A classification of related mammal species into TOL and INT types is likely to be too simple when more than two related species are compared (Happold, 1976a). For example, if this study had compared the behaviour of three vole species, a TOL species, an INT species and an intermediate would probably

have been found. The ability to define the magnitude of species differences in bodily contact and salient contact-promoting behaviours may allow us to understand better some of the bases for the many variations in the forms of social structure which distinguish mammal populations and species.

I feel that a major strength of this study is that observations have not been restricted to any one functional category of behaviour, such as play or parental care-giving behaviour. Only some of the body nosing behaviour by young animals described in this study could be assigned to the 'play' category by virtue of certain accompanying motor movements such as rotational head movement, jumping or running, and relaxed muscle tone during dyadic manoeuvering in the mutual-upright and other positions. Further, time spent by parents and young in bodily contact has been recorded in this study irrespective of time spent nursing and licking infants; thus the social relationship between parents and young rather than the parents' care-giving behaviour was being traced. This inclusion of body nosing and other contact behaviours that would usually fall outside the categories of play and parental behaviours has hopefully resulted in the study generating a more complete picture of juvenile social development than if only 'play' and 'parental care' had been recorded. For example, all the juvenile behaviours observed that involved contact are regarded as promoting juvenile socialisation; social play is regarded as episodic intensification of dyadic body nosing and manoeuvering, i.e. some aspects of the socialisation process.

Evidently play in these rodents can only begin to be understood if the significance of non-play body nosing (Mode I nosing in the Microtus, see Chapter 3) is first appreciated. When a young rodent noses another, it may be doing more than merely investigating or greeting. In fact, virtually all juvenile social interactions in the rodent species of this study were circumscribed by body nosing. A social interaction between two young may consist solely of a series of body nosing contacts to the same or varying parts of the body; the nosing may be mainly by one partner, or the two animals may nose turn about. Play by the young of these rodents in its relatively simple form may involve 1. speeding up of the rate of repetition of nosing, 2. simultaneous nosing by both partners, and 3. locomotor-rotational movements and increasingly relaxed muscle tone.

In Microtus it seems to the author as if Mode II (play) nosing interactions may relate to Mode I nosing similarly to the way in which running relates to walking (in any species): it achieves the goal more rapidly, but can only be sustained in short bursts, since much energy is expended. Possibly voles may engage in Mode II interactions when there is an urgent need to create, solidify or intensify a non-aggressive relationship.

The greater use by the octodontid young of physical manoeuvering is seen by the author as a step towards complexity in juvenile rodent interactions. Venter-to-venter interactions

occur during play (Mode II) interactions, but not at all during non-play, non-aggressive (Mode I) juvenile interactions. This is true of all four rodent species of this study, although the incidence of venter-to-venter interactions is very much higher in the Octodontids compared with the Microtus. The occurrence of venter-to-venter interactions in play therefore seems to mean more than just an intensification of Mode I behaviour, and to represent an increase in complexity and implication of the play interaction.

I feel that a further strength of this study lies in drawing attention to the significance of body nosing despite the absence of any anatomically distinct glands in the body regions nosed. There is a tradition growing in the mammal literature of research attending to the function of anatomically distinct skin glands (e.g. Murphy, 1970; Johnston, 1975; Clarke and Frearson, 1972; Müller-Schwarze, 1971; Quay and Müller-Schwarze, 1970; Stoddart, 1972 a, b; Thiessen et al., 1969; 1971; Sale, 1970; Schulze-Westrum, 1969), and this research has yielded many excellent results. However, I feel that it is important for research in this field to remain open and sensitive to the probable social importance in many species of skin odour in body regions where there are no distinct glands. None of the body regions nosed by the juvenile voles and Octodontids of this study constituted an anatomically visible gland, yet the young

animals behaved as if nosing of these areas was of the utmost significance in their social development.

To conclude, the author hopes that the slightly unconventional themes of this thesis may contribute a little towards focussing attention on some under-appreciated aspects of juvenile rodent behaviour which may become important in understanding both the development of contact-promoting behaviour in small mammals and differences in social structure between related species.

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APPENDIX

DEFINITIONS

The following are operational definitions of certain words used in the text of this thesis.

AGGRESSION 'Aggression' refers here to a type of social interaction in which at least one of the interactants behaves in such a way as to repel, injure, immobilise, or restrict the movements of another conspecific. The behaviour may include chasing or physical manoeuvering, and the animals give the appearance of tense body tone.

DEFENSIVE 'Defensive' is used here to qualify social behaviour which involves jerky, hesitant, warding and sometimes withdrawal movements by at least one of the interactants with regard to the other.

AMICABLE 'Amicable' is used here to qualify social behaviour which involves docile contact between interactants who do not attempt to repel, injure, immobilise, or restrict the movements of each other.

ALLOGROOMING One animal licks or nibbles another's fur in a docile manner.

PLAY 'Play' refers here to amicable (as defined above) social interaction involving quick body movements, rapid progression from one act to the next, and either physical manoeuvering (such as in the mutual-upright position) or locomotor-rotational movements (such as jumping or head-shaking). The animals give the appearance of relaxed body tone.

Mode I interactions (Chapter III) are amicable social interactions between young voles which involve body nosing without satisfying the 'play' criteria as defined here. Mode II interactions differ from Mode I in that the animals' movements satisfy the criteria for 'play'.

SOCIALITY Sociality refers here to a tendency for conspecifics to maintain proximity to one another.

OLFACTORY EXCHANGE The exchange of information contained in the chemistry of the animals' body secretions when the animals nose one another's bodies.